

JOURNAL OF

THE ROYAL SOCIETY

OF

WESTERN AUSTRALIA

VOLUME 54

PART 1

1971

THE
ROYAL SOCIETY
OF
WESTERN AUSTRALIA

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1.—Petroleum Exploration in Western Australia; Past, Present and Future

Presidential Address, 1970

by Phillip E. Playford

Historical Review

Interest in finding oil in Western Australia was first aroused soon after the turn of the century, when supposed traces of oil were reported from the Warren River area, near the south coast. Three holes were drilled during the period 1902-04, but without success. Since this first short-lived boom there have been many ups and downs in oil exploration, and it was not until 1967, 65 years after the first well was drilled, that commercial production began in this State, at Barrow Island.

The main turning points for oil exploration in Western Australia were the discoveries at Rough Range in 1953, and at Barrow Island in 1964. Prior to the Rough Range find many sceptics maintained that oil could not be found in this State, and this discovery did a lot to encourage people, not only among the general public, but also among professional oil men, that commercial fields could indeed be found. Barrow Island was of course even more important, as it was the first oil discovery to be proved commercial.

After the Warren River drilling there was little further activity until 1918, when traces of oil were reported from a water bore being drilled on Gogo Station in the Kimberley district. This report was confirmed by a geologist, and as a result the Freney Kimberley Oil Company was formed to prospect for oil in the Kimberleys. The company drilled a number of holes between 1922 and 1941, when it had to cease operations because of the war.

Modern exploration commenced in Western Australia in 1952, when West Australian Petroleum Pty. Ltd. (Wapet) began operations. This company had been formed to take over permits that had been acquired by Ampol in 1947.

The company had dramatic success in December 1953 with its first well, Rough Range no. 1. Great hopes were held that large commercial fields would be proved in the Exmouth Gulf area. However, subsequent drilling showed that the Rough Range field covers only a few acres and is non commercial. Had the well been drilled on the original site selected by geologists it would have been dry, but it was moved a few hundred feet for easier site preparation, thus placing it exactly over the tiny field. This was a piece of "luck" that was financially unfortunate for the company, as it resulted in a great deal of dry-hole drilling that would never otherwise have occurred. However, although Rough Range was not a commercial success, it spurred exploration throughout Australia.

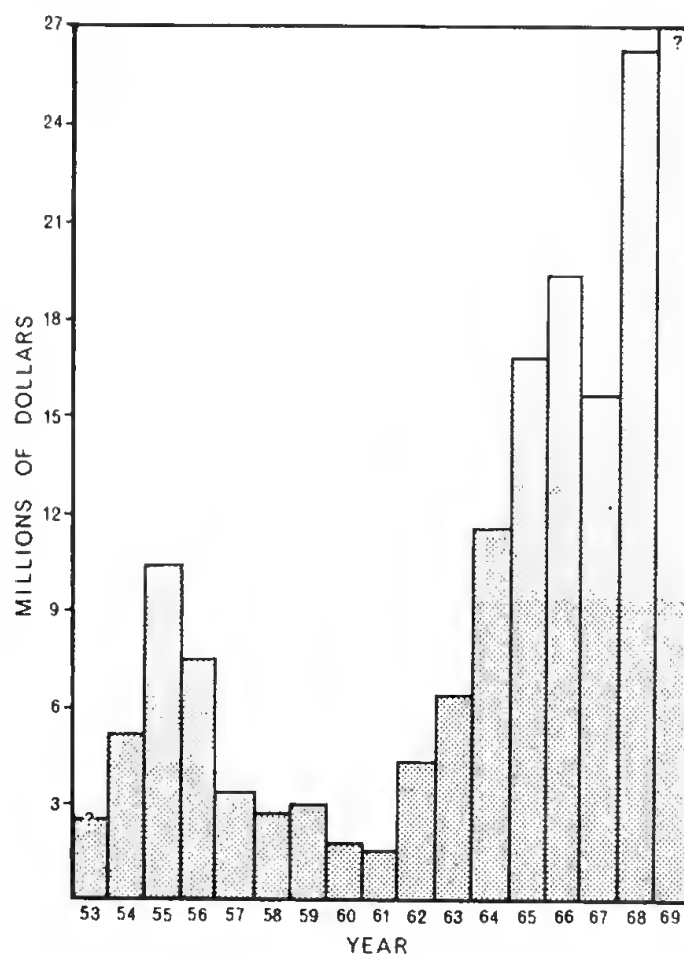


Figure 1.—Petroleum exploration expenditure in Western Australia, 1953-1969.

During the period of enthusiasm after the Rough Range discovery, exploration expanded throughout the State's sedimentary basins. However, this enthusiasm waned with the lack of further success in the Exmouth Gulf area, and no additional fields were found elsewhere in the State. Over the next 8 years exploration gradually tailed off, until the trough was reached in 1961 (figures 1 and 2). Then in that year oil was found at Moonie in Queensland, and just as with Rough Range, this discovery stimulated exploration throughout Australia. Of course the Moonie find had no bearing on the oil prospects in Western Australia, but it is remarkable the psychological impact made by such discoveries, not only on the public, but also on the directors of some major oil companies. Consequently, the Moonie discovery was followed by an increase in exploration expenditure in Western Australia, and this led up to the Barrow Island discovery in 1964. Barrow Island proved

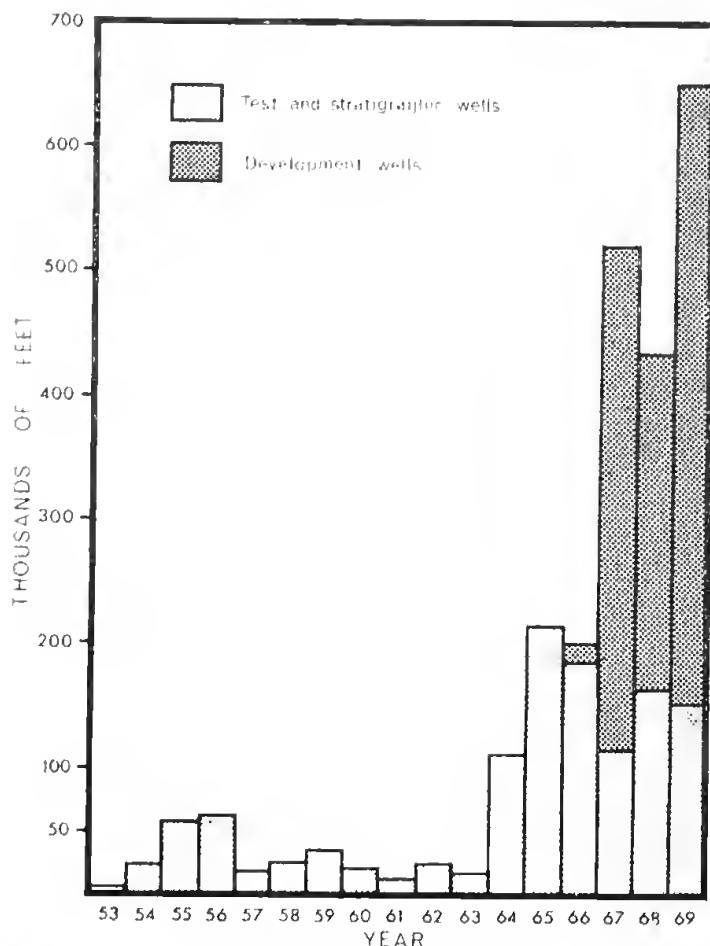


Figure 2.—Petroleum drilling in Western Australia, 1953-1969.

to be the State's first commercial field; the initial shipment of crude oil leaving the island in 1967. Actually a few months before this discovery oil and gas had been found at Yardarino in the Perth Basin. Yardarino is only a small field, but it will be developed commercially next year, as there are plans for linking it to the Dongara-Perth gas pipeline.

The Barrow Island discovery initiated the third period of exploration in Western Australia, which is continuing to the present. It has been marked by a big increase in expenditure on oil exploration and development in this State (figure 1). Several further discoveries have been made, notably those of gas at Dongara, Gingin, and Mondarra, all of which are to be developed for the Perth-Kwinana-Pinjarra market. The pipeline from these fields is expected to be completed late in 1971.

Another significant discovery of oil was made in 1968 in Legendre no. 1, the first offshore well drilled in the State. Today the major part of expenditure on exploration in W.A. is in the offshore areas, which probably have the best potential for future major discoveries.

More detailed information on the history of petroleum exploration in Western Australia is contained in the following publications: Hobson (1936), Playford and Johnstone (1959), Bureau of Mineral Resources (1960), and Playford (1966). The stratigraphy and structure of the sedimentary basins of the State is summarized by McWhae and others (1958).

Exploration Permits

Nearly all of the prospective sedimentary areas of Western Australia are covered by petroleum exploration permits. The principal permit holder is West Australian Petroleum Pty. Ltd., which has farmed out large areas to Continental, Total, and Union. Other large permit holders are the B.O.C.-Woodside-Mid Eastern-Shell-BP-Calasia-tic consortium, which holds large areas of the continental shelf in the Carnarvon, Canning, and Browse Basins, and the Arco-Aquitaine partnership, which holds much of the offshore Bonaparte Gulf Basin.

The offshore permits are controlled jointly by the State and the Commonwealth. Under the terms of the Petroleum (Submerged Lands) Act, 1967, offshore permits may cover no more than 400 5-minute blocks, or about 10,000 square miles. The initial period of tenure for each permit is 6 years, and at the end of that period 50% of the area must be relinquished, with further 50% relinquishments of the remainder after each succeeding 5-year period. The onshore areas are controlled by the Petroleum Act, 1967, which is only now being implemented. Permits may cover no more than 200 blocks or about 5,000 square miles. After the initial tenure of 5 years 25% of each permit must be relinquished, with further 25% relinquishments (of the total original area) after each succeeding 5-year period. Both onshore and offshore permits carry specified work commitments which must be met year by year.

In the long term the effect of these acts should be to spur exploration throughout the State. Very large permits have been held for many years by companies that have done little or no work over big portions of their concessions. This will no longer be allowed now that the permit areas are to be broken into smaller blocks which will have to be either explored systematically, or relinquished. The most effective way for a company to continue holding an interest in an area on which it cannot or does not wish to spend further money is to arrange a farmout. As a result we can expect that more farmout deals will be made in Western Australia during the next few years.

Figure 3 shows the Phanerozoic sedimentary basins of Western Australia and the positions of exploratory wells that have been drilled.

Sedimentary Basins

The sedimentary basins cover about 43% of the land area of the State and about 90% of the continental shelf. This is a total area of about 650,000 square miles. More than half of this, in the Bonaparte Gulf, Browse, Canning, Carnarvon, and Perth Basins, is believed to have moderate to good prospects for petroleum. The potential of the rest of the sedimentary areas is regarded as being low.

Perth Basin

The Perth Basin (figure 4) is a long narrow trough of sediments extending north-south for some 600 miles. The eastern boundary is the great Darling Fault, one of the major structural features of the earth's crust. The basin is strongly faulted throughout. Most faults have

WESTERN AUSTRALIA SEDIMENTARY BASINS

SCALE IN MILES
100 0 100 200 300

○ Exploratory well

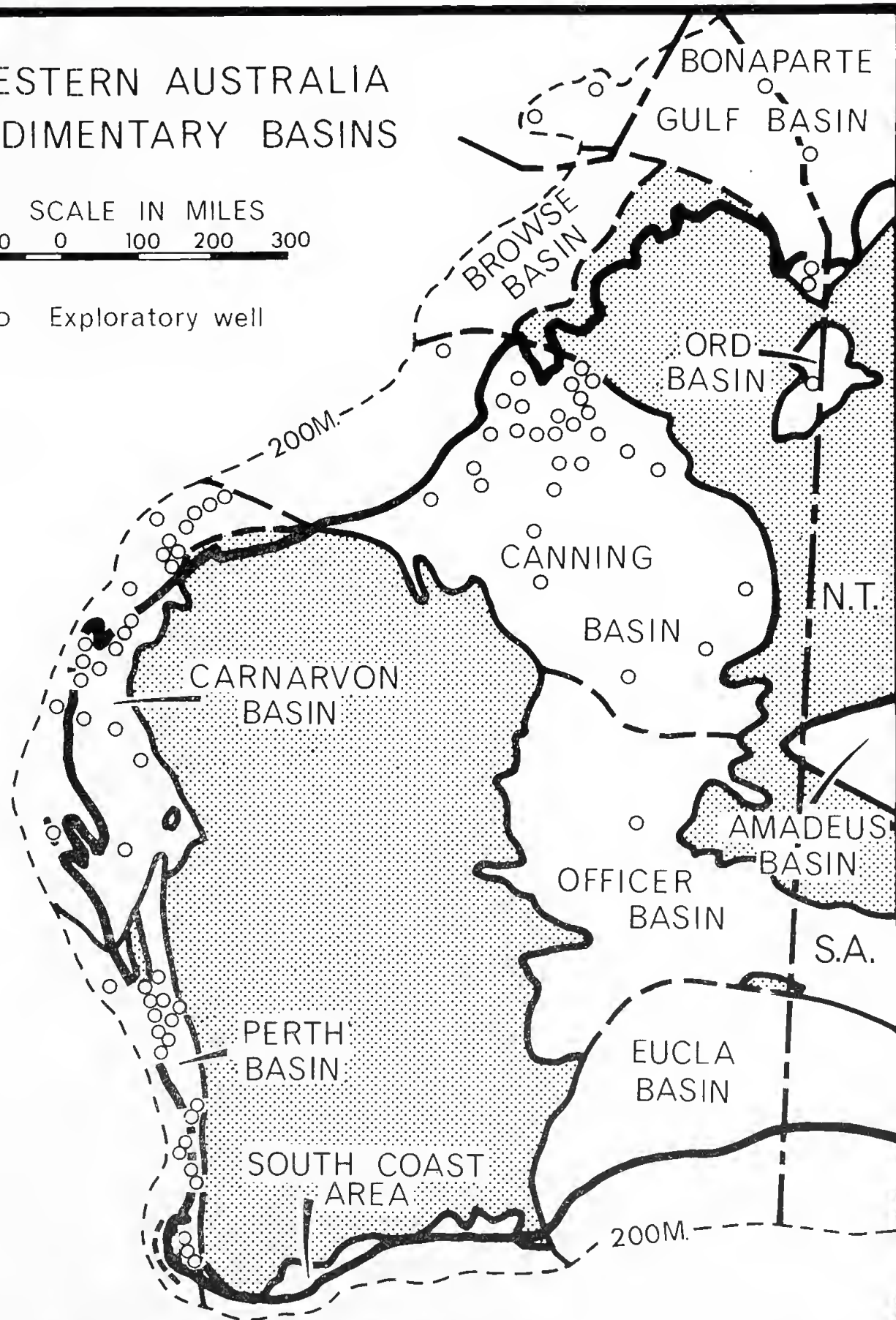


Figure 3.—Sedimentary basins of Western Australia.

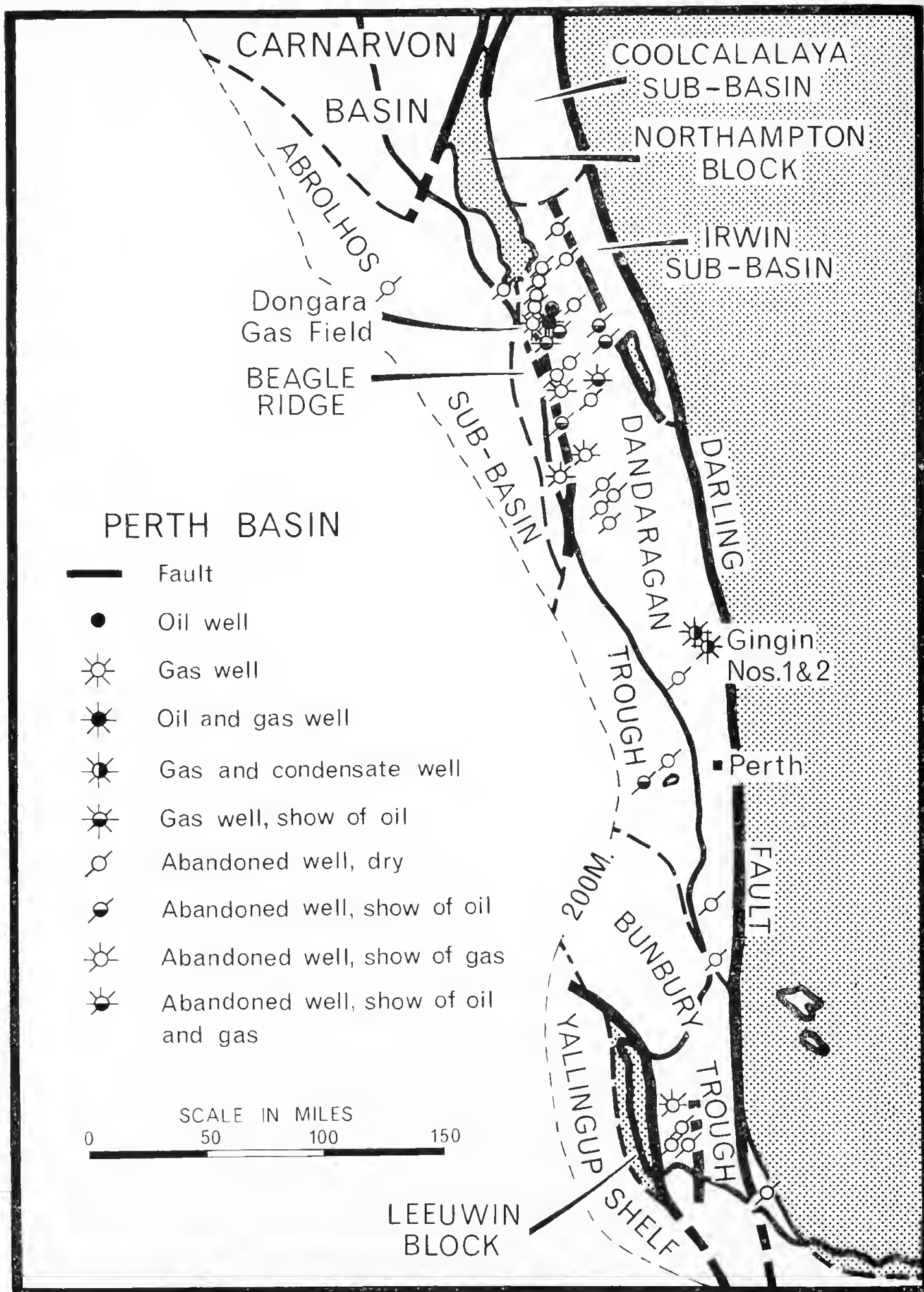


Figure 4.—Perth Basin, showing stratigraphic-structural provinces and exploratory wells.

northerly to north-northwesterly trends, and they are thought to have normal displacements. No simple anticlinal structures are known; those that have been recognized are associated with faults. The Gingin Anticline is the largest known structure in the basin, being about 30 miles long and having 4,000 feet of closure.

The total thickness of the Phanerozoic section in the Perth Basin probably exceeds 40,000 feet, and the sediments are of Silurian, Permian, Triassic, Jurassic, and Tertiary age. Much of the section is parallel to continental, the continental deposits being largely of fluvial origin, shed from the active Darling Fault. The best prospects are in the Cretaceous, Jurassic, Triassic, and Permian sequences.

The most important field found to date in the Perth Basin is the Dongara gas field (figure 5). All but 4 of the 19 wells drilled to date by Wapet at Dongara have produced gas or oil, with daily yields of up to 10 million cubic feet of gas and 1,400 barrels of oil. Production is obtained from the Lower Triassic Yardarino Sandstone and from sands in the Lower Permian Irwin River Coal Measures, at depths of around 5,500 feet. The field occurs in an anticlinal flexure covering about 10 square miles, bounded on the east by the Mountain Bridge Fault. This fault has a displacement (down to the east) of about 2,000 feet. The distribution of oil and gas wells in the field can probably best be explained by a combination of small-scale faulting and stratigraphic complications. Details of the structure are difficult to determine because of the poor results obtained from seismic surveys, resulting from a surface cover of Coastal Limestone.

Wapet, through its subsidiary Wang (West Australian Natural Gas Pty. Ltd.), has announced plans for development of the Dongara gas field for the Perth market. A 14-inch gas pipeline will be constructed to link the Dongara, Yardarino, Mondarra, and Gingin fields to Perth, Kwinana, and Pinjarra. The Company has announced that it has reserves sufficient to supply gas at 70 to 80 million cubic feet per day for 15 years. The reserves of the Dongara field (by far the largest of the fields to be developed) are believed to be about 500 billion cubic feet. These reserves are relatively small considering the potential of the industrial market around Perth, but more gas discoveries can certainly be expected in the northern Perth Basin. The reserves are nearly treble those of the Roma fields that supply Brisbane (about 180 billion cubic feet), but they are much less than those of the Moomba-Gidgealpa fields supplying Adelaide (about 1.4 trillion cubic feet), or the Bass Strait fields supplying Melbourne (about 3.5 trillion cubic feet).

The reserves of oil at Dongara are rather small, and the company has announced no plans for their commercial use.

The nearby Yardarino and Mondarra gas fields are much smaller than Dongara. Both produce from the Lower Triassic Yardarino Sandstone, at around 7,500 feet at Yardarino and 8,900 feet at Mondarra. The full extent of the Mondarra field has not yet been determined by drilling.

The Gingin gas and condensate field occurs in a very large anticlinal structure. Production is from low-permeability sands in the Lower Jurassic Cockleshell Gully Formation, between 12,680 and 13,630 feet in Gingin no. 1 and slightly deeper in no. 2. The first well was the best producer, yielding up to 3.84 million cubic feet of gas and 47 barrels of condensate per day. The permeability of the sands is very low, and production declined with prolonged testing, especially in Gingin no. 2. However, it has been reported that the Gingin field will also be tied to the gas pipeline. Production could possibly be stimulated by fracturing the low-permeability sands, but their depth poses technological problems. The productivity of the field cannot be reliably estimated at this stage.

Other small non-commercial discoveries have been made in the Perth Basin in Gage Roads no. 1 offshore well (oil, from the Lower Cretaceous South Perth Formation), Mt Horner no. 1 (oil, from the Lower Triassic Kockatea Shale), Arrowsmith no. 1 (gas, from the Lower Permian Carynginia Formation), and Whicher Range no. 1 (gas, from the Permian Sue Coal Measures). Minor quantities of oil and gas have also been obtained from a number of other wells.

The percentage of wells that have encountered showings of hydrocarbons is higher in the Perth Basin than in any of the other Western Australian basins, yet it was the last of the major basins in which serious exploration was commenced. The best prospects in the basin are probably in the Abrolhos Sub-basin, the northern and western parts of the Dandaragan Trough, and the northern part of the Bunbury Trough.

Carnarvon Basin

The Carnarvon Basin (figure 6) overlaps the Yilgarn Block on the east, and is limited by the continental slope on the west. It covers about 45,000 square miles onshore and 42,000 square miles offshore. The maximum aggregate thickness of sediments in the basin may exceed 65,000 feet, although the maximum thickness at any one place is probably not more than 35,000 feet. The sediments are of Silurian, Devonian, Carboniferous, Permian, Triassic, Jurassic, Cretaceous, and Tertiary age. Most of the section is marine, apart from a thick unit of sandstone of probable Silurian age at the base, which is interpreted as being at least partly continental. The Cretaceous and Jurassic sediments have produced oil and gas, and there are also prospects in the Palaeozoic and Triassic sequences.

The most conspicuous structural feature of the Carnarvon Basin is the series of anticlinal folds developed in Tertiary and Cretaceous rocks along the western margin, in the Gascoyne, Exmouth, and Barrow Sub-basins. The largest of these is Cape Range Anticline, which is 60 miles long and has a structural relief of some 1,500 feet. These structures are believed to have developed during a late Tertiary and Pleistocene period of compression. Much of the basin is strongly faulted. The boundary between the Wandagee Ridge and the Merlinleigh Sub-basin is one of the fundamental structural features of the basin. It is marked by an *en echelon* series of faults which throw down to the east, although

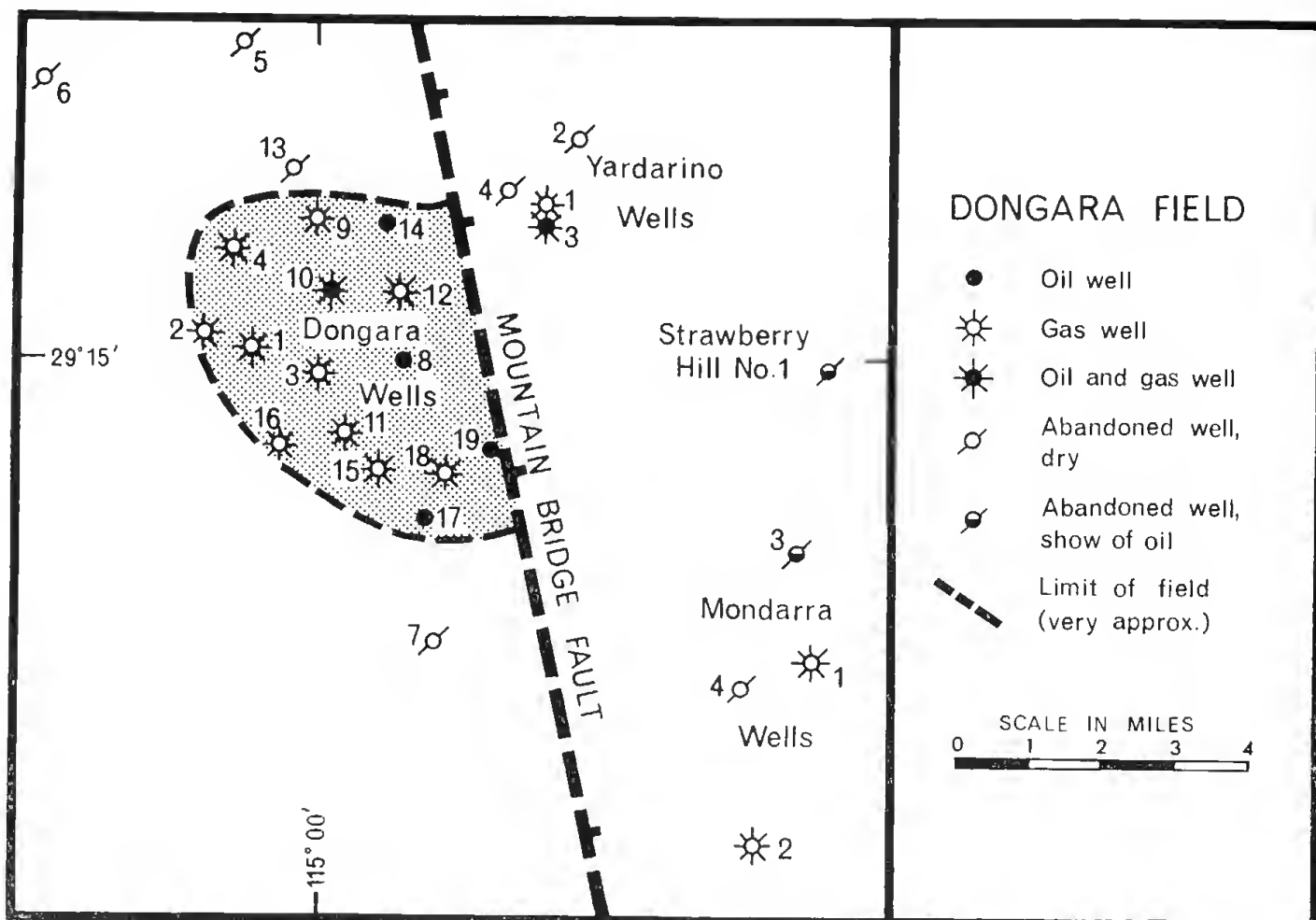


Figure 5.—Dongara gas field.

there has been a small amount of reverse movement (down to the west) along several of them in the late Cainozoic. The Merlinleigh Basin to the east is marked by thick Permian and Carboniferous deposits, and these are thin or absent along the Wandage Ridge and in the Gascoyne Sub-basin.

Exploration in the Carnarvon Basin was initially concentrated on the belt of Tertiary folds, especially those in the region around Exmouth Gulf (figure 7). As previously discussed, the Rough Range discovery was shown to be uneconomic. A lot of holes were also drilled without success on the huge Cape Range structure and in the intervening area between the two anticlines, although a moderate gas flow was obtained in one of the Cape Range wells.

Other surface anticlines to the south of Rough Range and Cape Range were drilled, but all proved to be dry. By 1958 only one major surface anticline remained, well to the north of Rough Range, at Barrow Island.

In 1964 a well was drilled near the surface culmination of the Barrow Island structure (figure 8), and it resulted in an oil discovery. The principal production was obtained from paralic Jurassic sands at about 6,700 feet. Subsequent drilling has shown that these sands are largely gas bearing and are discontinuous in distribution. However, during the drilling programme to evaluate the Jurassic reservoirs it was found that some thin low-permeability sands in the

Cretaceous sequence at around 2,000 feet could produce oil and gas. This reservoir is referred to as the "Windalia Sand", although it is now recognized as being part of the Muderong Shale. It has been developed as the main producing horizon at Barrow Island, yielding some 97% of the present daily production of 47,500 barrels. This field covers about 24,700 acres. It is limited to the south by a normal fault. The average thickness of the producing interval is 44 feet, and production is obtained from sands with permeabilities of 5 millidarcies or less. The in-place reserves amount to some 900 million barrels, and of this about 240 million barrels may be recovered. Production is stimulated by sand fracturing, and a secondary-recovery programme of water injection has been implemented. The oil is a light paraffin-base crude (36° A.P.I. gravity). The average production per well from the Windalia reservoir is about 145 barrels per day. In addition to the daily production (July, 1970) of 47,500 barrels of oil, the field also produces 28 million cubic feet of gas. The company has installed compressors for gas-lifting Windalia crude oil in some wells. To date (July, 1970) approximately 40 million barrels of oil and 28 billion cubic feet of gas have been produced. The maximum rate of production, 50,000 barrels per day, is expected to be reached later in 1970, when the full complement of 324 wells is in production.

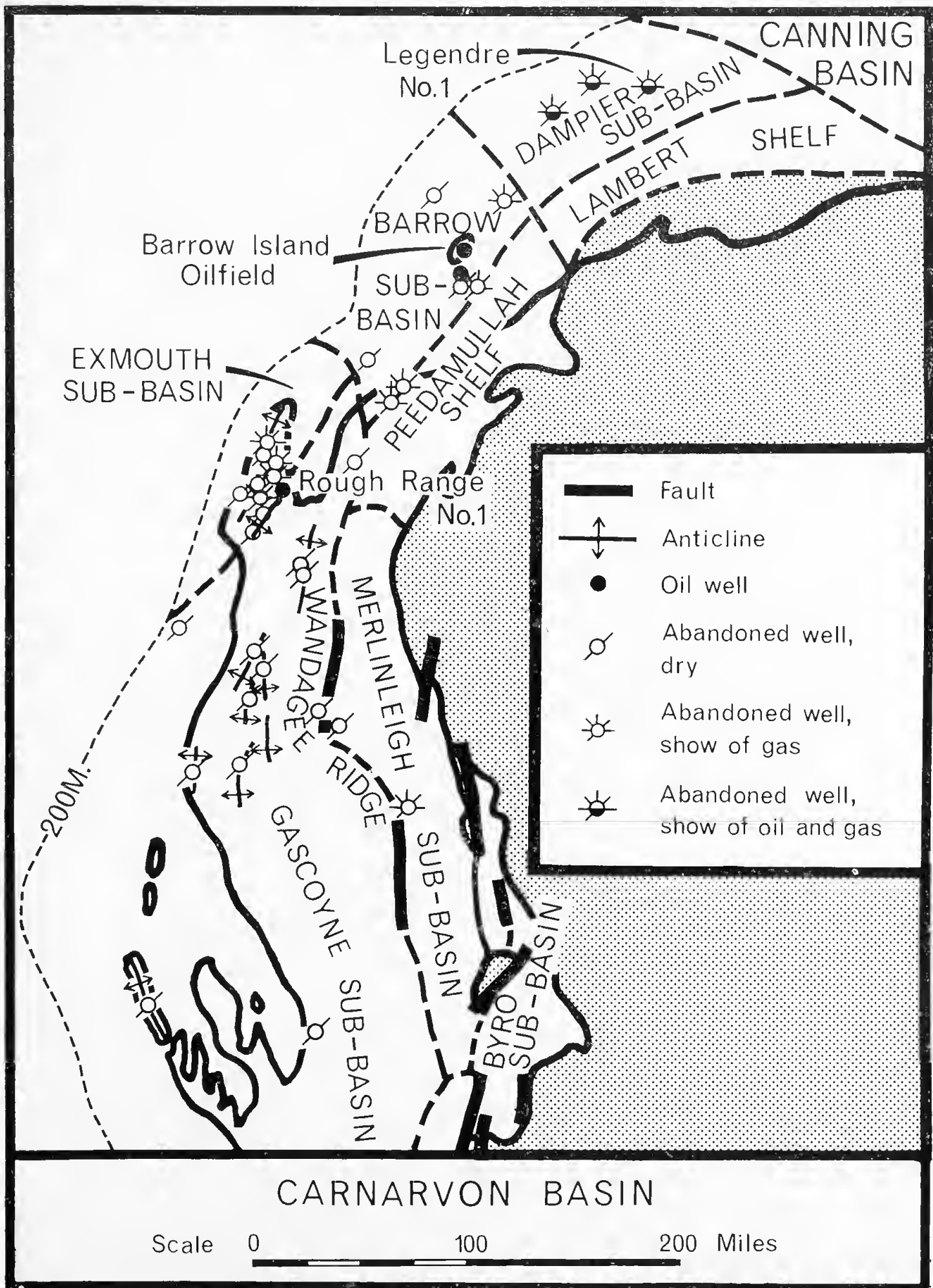


Figure 6.—Carnarvon Basin, showing stratigraphic-structural provinces and exploratory wells.

Oil discoveries have also been made just south of Barrow Island in the Pasco nos. 1 and 3 wells. They produce from Jurassic sands, but have not yet been developed commercially.

Another significant discovery was made by the B.O.C. consortium at Legendre no. 1 well (figure 6). It produced up to 1,014 barrels per day from around 6,200 feet in the Lower Cretaceous sequence. Although the well was abandoned as non-commercial because of the thinness of the producing sand, it is possible that other thicker sands will prove productive nearby. The Dampier and Madeleine wells drilled after Legendre had encouraging oil and gas showings from the Cretaceous and Jurassic sequences, but the section was tight. These wells have shown that a thick sequence of hydrocarbon-bearing sediments occurs in the Dampier Sub-basin, and there are good prospects that commercial production will eventually be obtained in the area. More drilling can be expected in the vicinity of Legendre and further to the southeast.

Wapet's exploration programme in the Barrow Sub-basin has been very disappointing since the Barrow Island discovery. It seemed very probable that oilfields would occur in some of

the anticlinal structures the company had defined by marine seismic surveys, but to date none have proved productive. Commercial fields should occur in this area, but it now seems that accumulations are more likely to be stratigraphic rather than structural.

The most likely areas in the basin for major oil accumulations remain in the Barrow and Dampier Sub-basins, despite the recent disappointments there. In addition to the Cretaceous and Jurassic, the Triassic is believed to have potential in those areas. Of the remaining provinces, the Exmouth Sub-basin, Peedamullah Shelf, and the offshore part of the Gascoyne Sub-basin probably have the best potential. Results of exploration in the rest of the basin have not been encouraging.

Canning Basin

The Canning Basin is the largest sedimentary basin in Western Australia, covering 160,000 square miles on land and 45,000 on the continental shelf (figure 9). The aggregate maximum thickness of Phanerozoic sediments in this basin may exceed 45,000 feet. The section is mainly marine and is of Ordovician, Silurian?, Devonian, Carboniferous, Permian, Triassic,

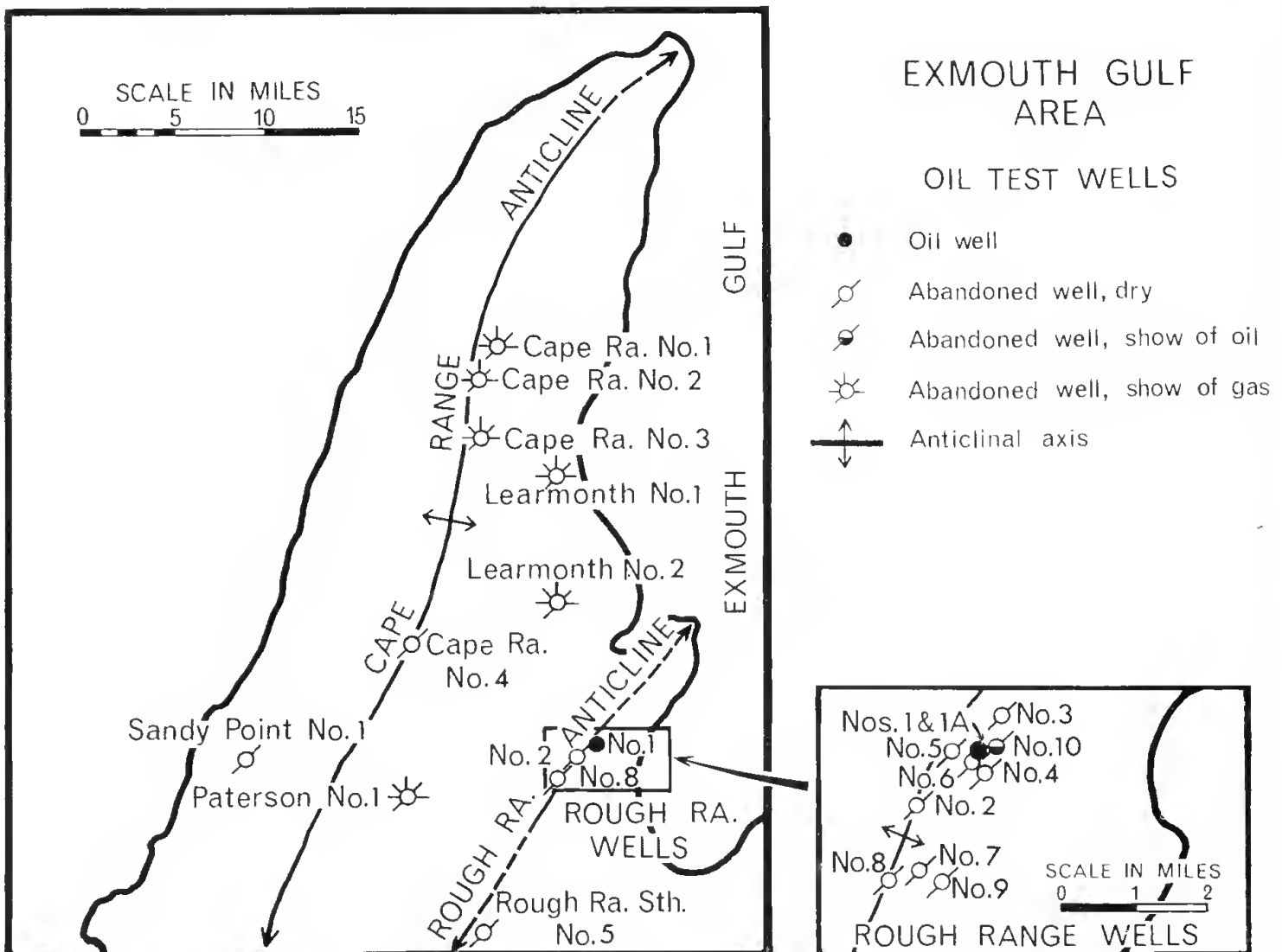


Figure 7—Exmouth Gulf area, showing exploratory wells.

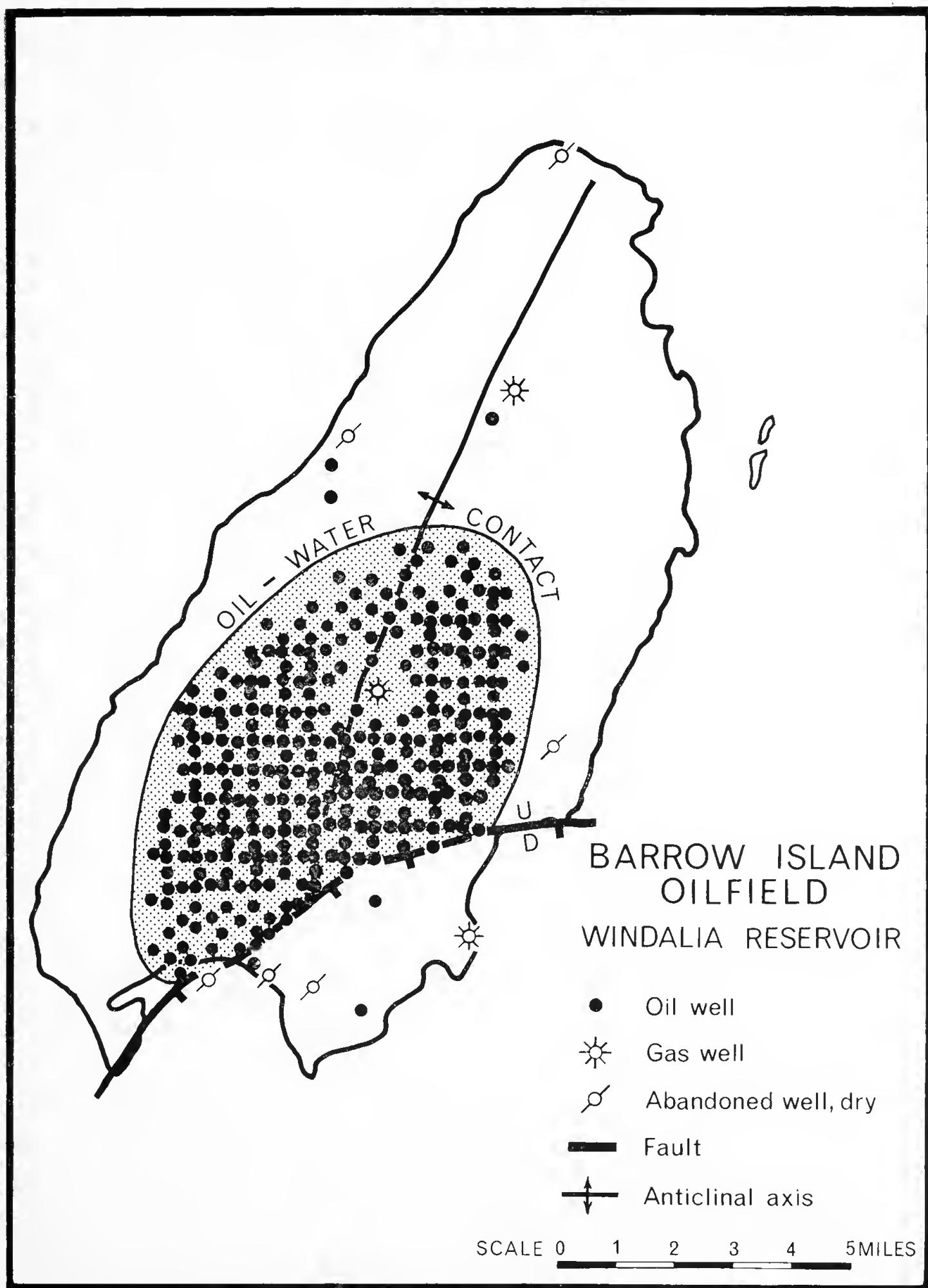


Figure 8.—Barrow Island oilfield.

Jurassic, and Cretaceous age. Tertiary sediments are believed to occur offshore. Exploration to date has been disappointing, and no fields have been found. However, this exploration is very thinly spread over such a huge basin, and with its thick sequence of marine sediments there should be some large fields. Encouraging showings of petroleum have been obtained from deposits of Ordovician, Devonian, and Carboniferous age. The Mesozoic section offshore is expected to closely resemble that of the northern Carnarvon Basin, and is therefore likely to have a high potential.

Exploration has been less intensive in the Canning Basin than in the Perth and Carnarvon Basins, and the stratigraphic-structural subdivisions shown on figure 9 are not well controlled.

Exploration was initially concentrated by Freney and Wapet on the large surface anticlines of the Fitzroy Trough, a deep graben containing thick Carboniferous and Permian deposits. Wells drilled to date have all been dry, and there is little incentive to drill further holes on the large anticlines. The best showings of oil and gas in the basin were obtained in Meda no. 1 well, drilled near the southern margin of the Lennard Shelf. A few gallons of oil were obtained from the Lower Carboniferous Fairfield Formation, and a small gas flow was obtained from the underlying Upper Devonian reef complex.

Minor showings of oil have been obtained from cores and cuttings of wells drilled in the Ordovician sequence of the Broome Platform.

From the limited amount of information available at present on the Canning Basin some generalizations can be made about the potential of the various provinces. The best prospects may be offshore, especially in the Mesozoic sequence. The Fitzroy Trough appears to be a poor prospect, as already discussed. The Devonian reef complexes of the southern margin of the Lennard Shelf are believed to have moderately good prospects, as is the Jurgurra Terrace. There has been some encouragement on the Broome Platform, and parts of it may have moderate prospects. Too little is known about the Kidson Sub-basin and the Ankettell Shelf to satisfactorily appraise their potential.

Bonaparte Gulf Basin

The Bonaparte Gulf Basin is partly in Western Australia and partly in the Northern Territory and the Commonwealth Territory of Ashmore and Cartier Islands (figure 10). Only a small part of the basin lies onshore, and most exploration has been concentrated on the continental shelf. The maximum aggregate thickness of sediments in the onshore part of the basin is about 19,000 feet, and at least an additional 15,000 feet is thought to occur offshore.

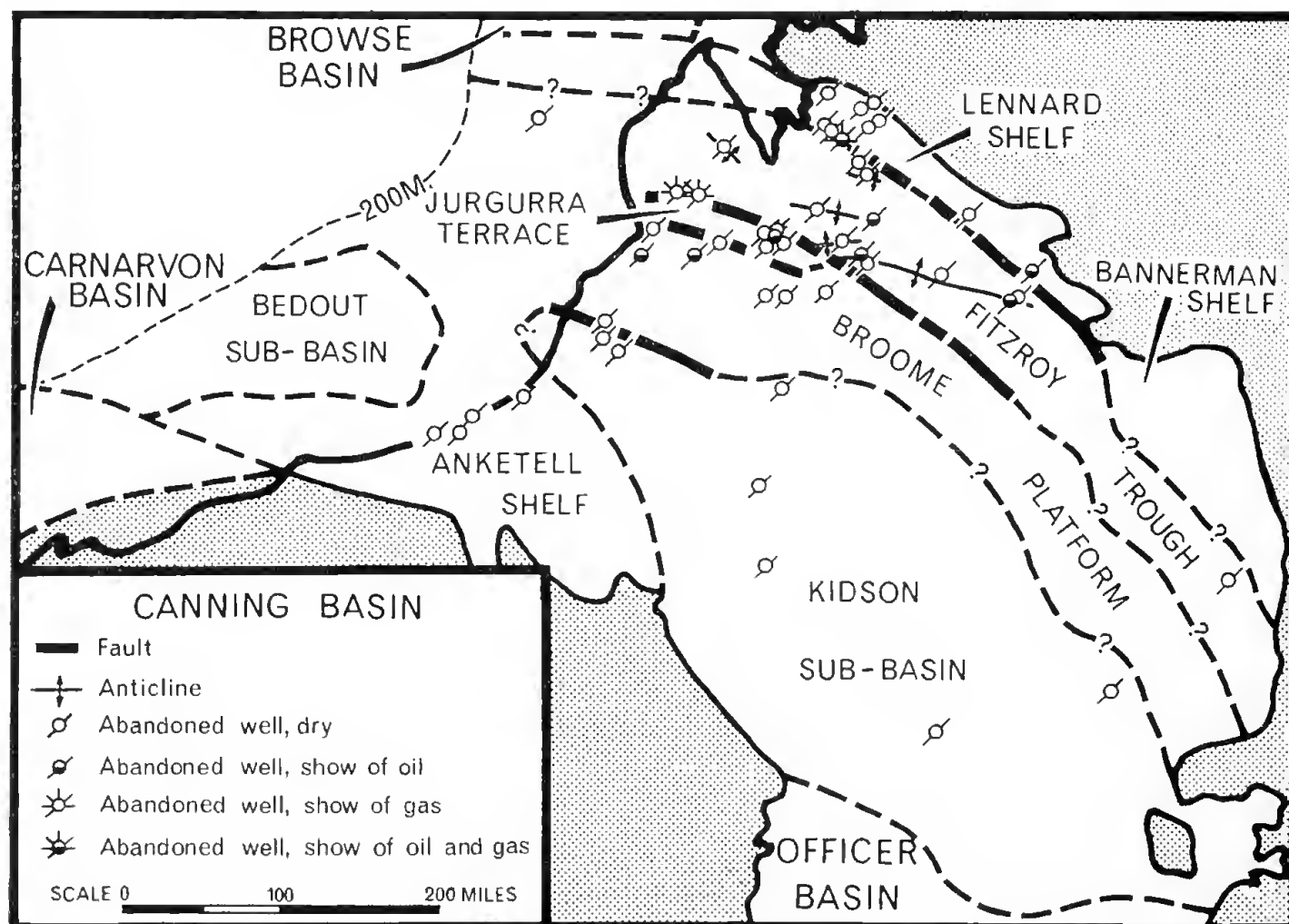


Figure 9.—Canning Basin, showing stratigraphic-structural provinces and exploratory wells.

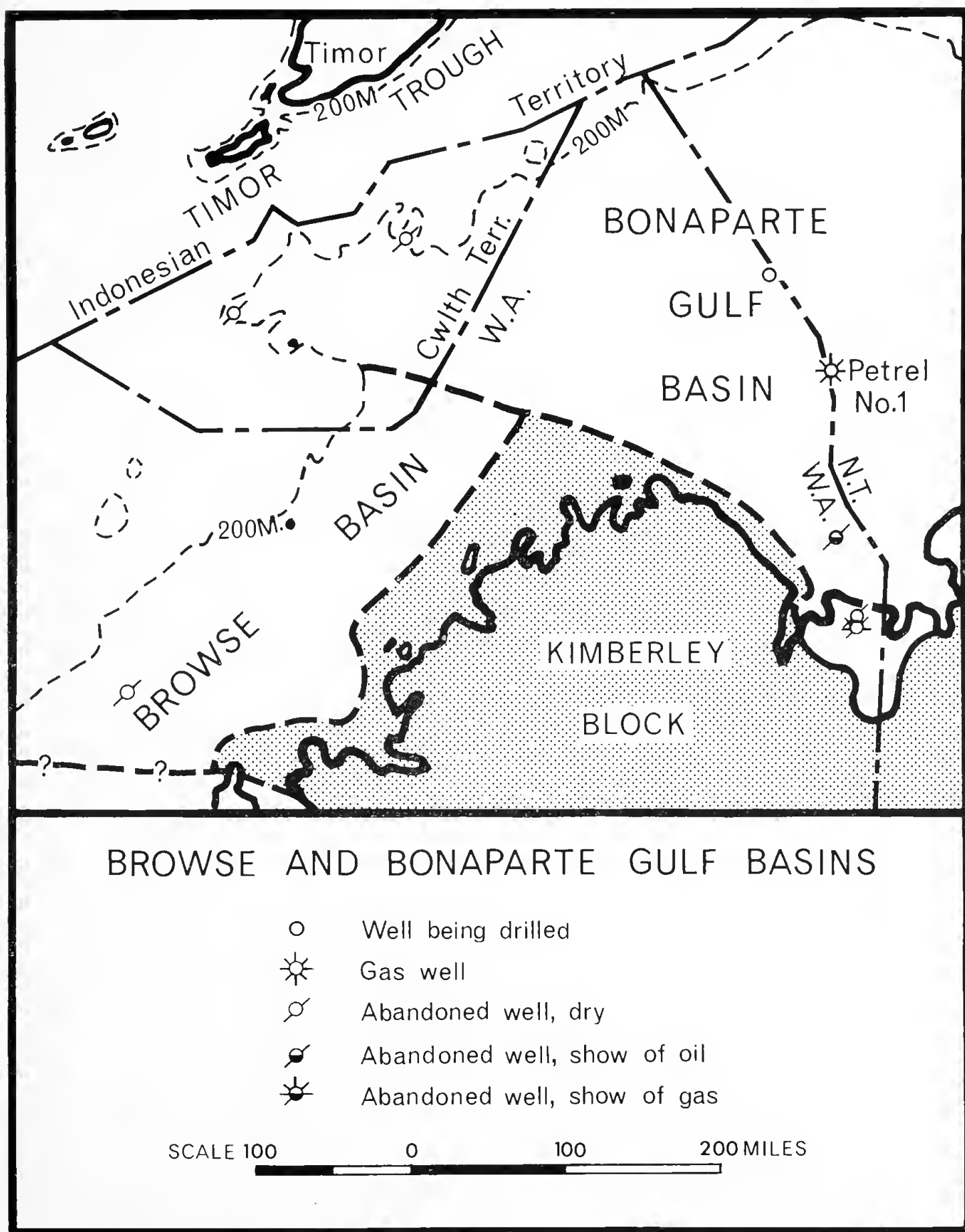


Figure 10.—Browse and Bonaparte Gulf Basins, showing exploratory wells.

The rocks are of Cambrian, Ordovician, Devonian, Carboniferous, Permian, Triassic, Jurassic, Cretaceous, and Tertiary age. The best prospects are believed to be in the Devonian, Carboniferous, Permian, and Mesozoic sequences.

Exploration has been conducted on a limited scale in the onshore Bonaparte Gulf Basin in Western Australia. The quality of seismic data has been poor, and the two test wells drilled, Bonaparte nos. 1 and 2, were not structurally well controlled. Bonaparte no. 2 had a small gas flow, but it was abandoned as non-commercial. One offshore well has been completed in Western Australian waters, Lacrosse no. 1, and this had encouraging oil shows in the Permian sequence. Another well, Gull no. 1, is being drilled by Arco-Aquitaine. The two wells drilled in the Territory of Ashmore and Cartier Islands, Ashmore Reef no. 1 and Sahul Shoals no. 1, had no significant hydrocarbon shows. However, an important gas discovery was made in Arco-Aquitaine's Petrel no. 1 well, just over the border in Northern Territory waters. This well blew out at a depth of 13,057 feet in Upper Permian rocks. The gas is dry, and the well is blowing at a rate of several million cubic feet per day. A relief well, Petrel 1A, is being drilled nearby, and it is hoped to kill the blowout late in 1970.

The offshore Bonaparte Gulf Basin is believed to have a high potential for the discovery of major petroleum reserves.

Browse Basin

Available data on the Browse Basin are rather meagre. Geophysical results suggest that the basin contains up to 20,000 feet of Phanerozoic sediments (presumably Tertiary, Mesozoic, and Palaeozoic). One dry well, Leveque no. 1, has been drilled, but details of the section penetrated have not yet been made public.

Ord Basin

The Ord Basin in Western Australia and the Northern Territory contains 2,500 feet of Cambrian and Devonian? sediments resting on basalts of probable Lower Cambrian age. One of the first oil test wells drilled in Western Australia, the Okes Durack bore, was put down on an anticline in the basin during 1924. It was dry, and there has been no further exploration since then.

Amadeus Basin

Very little of the Palaeozoic Amadeus Basin extends into Western Australia, and this part is believed to have no petroleum prospects.

Officer Basin

The Officer Basin occupies some 120,000 square miles in Western Australia, and a further 30,000 square miles in South Australia. The total thickness of sediments in the Western Australian part amounts to at least 20,000 feet, but only 3,000 feet of this is known to be Phanerozoic, consisting of Permian, Jurassic, and Cretaceous deposits. The underlying section has been presumed to be Proterozoic, but it is possible that part is in fact older Palaeozoic.

Hunt Oil Company carried out extensive geophysical exploration in the Officer Basin from 1961 to 1966. The company also drilled four stratigraphic wells and put down a single test well, Yowalga no. 2, in 1966. As this well encountered presumed Proterozoic rocks at shallow depth, Hunt decided to withdraw from the area.

Despite the discouraging results of the Yowalga well, the oil prospects of the Officer Basin cannot be completely written off, although they must be regarded as low.

Eucla Basin

The Eucla Basin contains a thin sheet of Cretaceous and Tertiary sediments, having a maximum thickness of 3,000 feet (in the offshore part). Three stratigraphic wells have been drilled, and there has been a small amount of geophysical exploration. The conclusion reached was that the section is everywhere too thin and lacking in structure to have any oil prospects. Attention then turned to the continental shelf, where Tenneco carried out a marine seismic survey. This work showed that the offshore section is also thin and lacking in structure. The thickest section, amounting to about 3,000 feet, occurs in a channel or graben near the shelf margin. The Genoa-Hartog group has recently conducted a seismic survey over this feature.

Future Exploration

Most exploration today in Western Australia is being carried out in the offshore areas, but it is expected that activity will increase onshore once the exploration permits are finalized under the new Petroleum Act.

Moving now to the future, I am optimistic that large reserves of petroleum will eventually be found in Western Australia. The State's sedimentary basins cover extensive areas and contain thick accumulations of sediments, most of which are marine. No-one can claim that oil has been easy to find in these basins to date, but on a statistical basis they would be expected to contain large reserves of oil and gas.

One thing is clear; exploration should intensify in this State during the next few years. World-wide the consumption of oil is doubling every 10 years. Over the next 20 years it has been estimated that the world will consume about 500 billion barrels of oil and 750 trillion cubic feet of gas, which is about equal to all the present known reserves of oil and 75% of the gas. In order to keep pace with consumption and maintain a comparable reserves-to-production ratio as that held today, it will be necessary for the oil industry in the next 20 years to find about 3 times as much oil and gas as has been found in the past 100 years. In order to obtain and maintain self-sufficiency in Australia it has been estimated that we need to find about 20 billion barrels of oil in the next 20 years. This compares with the country's present known reserves of about 1.8 million barrels.

With this great need for further discoveries there must be an increasing interest in the prospective areas of Australia. Many petroleum geologists, including myself, regard Western Australia

lia as having the best potential for future discoveries in the Commonwealth. Large areas of our sedimentary basins are still relatively unexplored, and in only a few areas has there been really intensive exploration. Consequently the tempo of exploration in the major sedimentary basins of the State should increase significantly during the next 10 years. On the basis of present knowledge the best prospects for future discoveries appear to be on the continental shelf in the Perth, northern Carnarvon, Canning, and Bonaparte Gulf Basins, although some onshore parts of these basins are also very promising. I believe that there are excellent prospects for the future discovery of substantial oil and gas reserves in these areas.

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2.—An oval australite core from Lake Ballard, Western Australia

by W. H. Cleverly*

Manuscript received and accepted 18 July, 1970.

Abstract

An australite core from Lake Ballard weighs 200.29 g and is the fourth australite of weight exceeding 200 g known from Western Australia. From the radii of curvature of the posterior surface of the core the volume of the primary spheroid has been calculated as approximately 268 cubic centimetres. About 69% of the volume of the primary spheroid and 44% of its thickness have been lost by the action of processes operating during atmospheric flight and by subsequent terrestrial erosion.

Introduction

A large australite core was found by Mr. L. P. Berryman in May, 1968 on the dry floor of Lake Ballard and near its western end. The site of discovery is 107 miles N.N.W. of Kalgoorlie and has approximate co-ordinates 120° 36' E., 29° 21' S. Some small chips (possibly aggregating 0.1g) were broken from the core by rough handling before the nature of the find was understood.

The weight of the cleaned core is 200.29 grams. It is the fifth heaviest australite known to science, three heavier ones being known from Western Australia, and another from South Australia.

The locality of the find is 165 miles N.E. of Warralakin in what may be regarded as an extension of a known area of concentration of large australites (McCall 1965; Baker 1966, 1967). This concentration tends to assume the form of a belt athwart the australite strewn-field. The other three Western Australian australites of weights exceeding 200 g were found within this belt near Warralakin, Newdegate and Lake Yealering; their sites and those of other large Western Australian australites have been figured by McCall (1965) and Baker (1967).

Morphology and surface features

The core is slightly oval in plan view (Fig. 1A), the anterior surface (which faced earthwards down the flight path) merging into a flaked equatorial zone which terminates rearward at an illdefined rim (Fig. 1B); the rim separates the flaked equatorial zone from the posterior surface (an eroded remnant of the surface of the parental spheroid).

Two curved and roughly lozenge shaped flakes (38 x 17 and 31 x 17 mm), which may have attained 3 mm thickness at their centre points, and two smaller flakes have been lost from around the rim; the scars incline toward the posterior surface at an angle flatly oblique to the equatorial zone. Another scar overlaps the flaked equatorial zone from the anterior surface and represents the loss of a thin but extensive

flake (35 x 18 mm). The surfaces of the scars are completely frosted and the outlines smoothed; etched grooves are present, some being continuous with those of the posterior surface, but the depth of etching is not as great as on the two main surfaces.

The cause of this flaking (not to be confused with the loss of small flakes from the equatorial zone during flight) is unknown, but it is clearly not of recent date. Loss as a result of impact appears improbable; in most cases, blows would need to have been struck from the direction of the posterior surface to be effective. The two large rim flakes almost meet at a blunt point, and the possibility of "working" by aborigines was considered, but it is difficult to envisage a

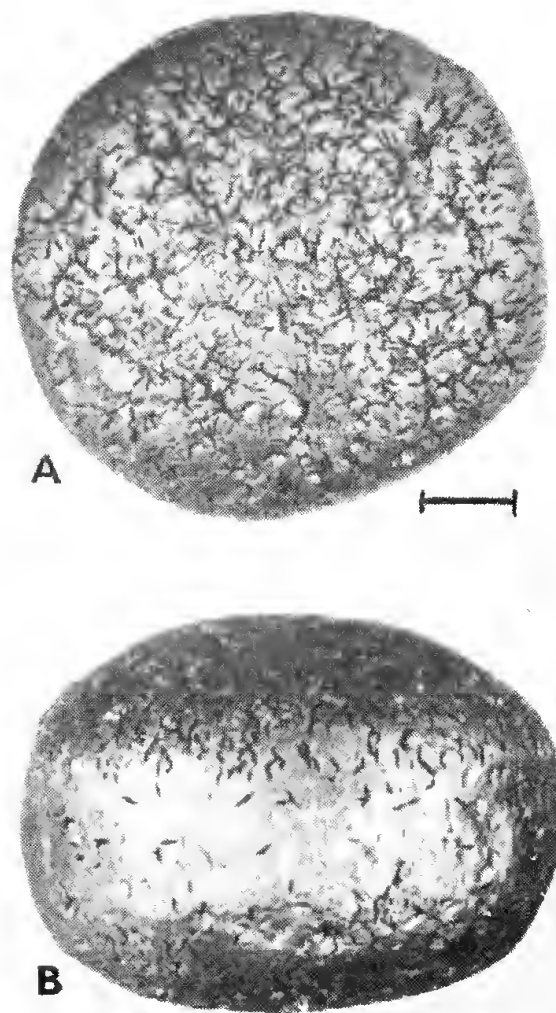


Figure 1.—The Lake Ballard oval australite core. A.—Posterior surface showing severe terrestrial etching effects. Angularity at lower right resulting from natural loss of two large flakes from the rim. B.—Side view, anterior surface at bottom of photograph. Left profile affected by natural flake loss. Scale bar one centimetre.

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use for an artefact with such a blunt and asymmetrically disposed point, except perhaps as a lethal stone (death pointer) or a punishment stone (Baker 1957); the "point" is undamaged by percussion. Natural spallation after landing seems most likely, followed by natural solution-etching and some mechanical abrasion.

Terrestrial abrasion and solution etching have been understandably severe because the site of find is a lake basin subject to the periodic drying out of saline and gypseous water; temperature ranges in the region are large: blown sand is an active abrading agent on the floors of such lakes. The lustre of the core is uniformly dull and the finer sculptural details usual on well preserved australites are absent.

The posterior surface is dominated by etched grooves of V-shaped cross section, often attaining one mm deep, occasionally solitary or in radiating "birdtracks", but united over most of the surface into a continuous crazed pattern which leaves small rounded or reduced plateau remnants of the original surface; etched lunate or circular "bruise marks" and small pits are recognisable only near the rim.

Smoothly scalloped areas on the flaked equatorial zone represent loss of flakes during the end stages of atmospheric flight and subsequently after landing as a consequence of spallation of the aerothermal stress zone—c.f. Baker (1963b). Grooves on this zone are shallow, about 1 mm wide, U-shaped in section, and have smoothed outlines; most are parallel to the line of flight and some extend over the full width (12–15 mm) of the flaked equatorial zone. There are numerous shallow pits, rarely attaining 1 mm diameter.

The anterior surface is less severely etched than the posterior surface and has a "birdtrack" pattern of grooves, several etched "bruise marks", and shallow pits distributed sparsely over the whole surface.

The etched pattern is distinctly radial near the edges of both the anterior and posterior surfaces. It is therefore likely to have been initiated by a process which affected the mass as a whole (such as the etching out of more susceptible schlieren related to rotation of the primary mass) rather than to radial streaming during atmospheric flight, which would have affected the anterior surface preferentially.

Dimensions of the core and the primary mass

The dimensions of the core are 60 x 57 x 44 mm thick. The thickness is greater than that of any of the large cores listed by Baker (1966), though considerably exceeded by that of the Newdegate core (Western Australian Museum No. 12318), which has a thickness of more than 52 millimetres.

Radii of curvature along the shorter and longer oval axes of the anterior surface (R_F) and posterior surface (R_B) were measured from enlarged silhouettes (c.f. Baker 1956 p. 57), but because of severe etching and erosion effects, the radii must be regarded as approximate. The values are:—

$$R_F = 39\text{mm and } 47\text{mm}$$

$$R_B = 39\text{mm and } 42\text{mm}$$

Assuming that the primary australite form was a biaxial ellipsoid with the same radii as the posterior face of the core, it would have had dimensions 7.8 x 7.8 x 8.4 cm and a volume of 268 cm³ (nearly).

Losses from the primary form

The volume of the remnant core is 82.27 cm³ and its thickness is 44 millimetres. About 69% of the volume and about 44% of the thickness of the primary form have therefore been lost by processes operating during atmospheric flight, by flaking of uncertain cause, and by terrestrial abrasion and solution etching.

The flaking is estimated to account for less than 1% loss. Terrestrial losses are difficult to assess, but they were certainly significant. It may be suspected from the intensity of etching towards the centre of the posterior surface that the arcs of curvature of that surface have been somewhat flattened and the radii of curvature increased; the volume of the primary spheroid might therefore have been over-estimated and thus also the percentage losses. The evident asymmetry of the anterior surface may be attributed to terrestrial processes because the presence of such asymmetry during atmospheric flight would have led to instability, for which no evidence was noted.

The percentage losses in forming the Lake Ballard core are greater than those for the Warralakin core (Baker 1962b), and it is also clearly evident from inspection that they were much greater than for the Newdegate core, the unusually deep form of which has been aptly described by McCall (1965) as "globular". Losses were, however, less than those for the Graball core and less than the mean losses for the well preserved Port Campbell cores (Baker 1963a, 1962a).

Such variable volume losses are attributable to a combination of different amounts of abrasion and/or solution etching according to different degrees of terrestrial erosion, coupled with differential aerodynamic ablation and fusion stripping of primary forms of somewhat different size and slightly varying angles of transit through the atmosphere.

Refractive Index and Specific Gravity

The glass constituting the core from Lake Ballard is translucent, smoky, and yellowish on thin edges. A minute flake from the chipped posterior surface is isotropic and has $N_g = 1.512$

A single inclusion noted in the flake is oval in section and has dimensions 75 x 33 microns. It is isotropic and of distinctly lower refractive index than the enclosing glass: it is probably lechatelierite.

The specific gravity of the core ($T_{120} = 20^\circ\text{C}$) is 2.435.

The specific refractivity is 0.2103.

TABLE 1

Comparison of Graball and Lake Ballard australite cores

	Graball core	Lake Ballard core
Primary body, radius, cm	8	7.8 x 7.8 x 8.4
Primary body, volume, cm ³	268	268
Specific gravity, core	2.434	2.435
Volume loss (all causes), %	74	69
Thickness loss (all causes), %	43	44

Conclusions

The Lake Ballard australite shows the usual features of large cores and a complex pattern of natural solution etch-grooves. As indicated in Table 1, there are points of close resemblance to the large round Graball core (Baker 1963a), from which it differs principally in having been derived from an imperfectly spherical parent mass and in its somewhat smaller losses during atmospheric transit. Because terrestrial losses have been especially severe when compared with the "reasonably well preserved" Graball core, the Lake Ballard loss figures should be reduced somewhat before making a comparison of atmospheric losses.

The chance discovery of the Lake Ballard core by a member of a mineral exploration party confirms the existence of a Western Australian concentration of unusually large australites and suggests that this concentration may take the form of a more or less meridional belt across

the strewnfield. However, so much of the area has been so imperfectly collected, that it would be unwise to draw further conclusions.

Acknowledgments

I am grateful to Mr. L. P. Berryman for the loan of the australite for examination, to Dr. George Baker for his careful reading of the manuscript and constructive criticism, to Mr. T. G. Bateman for photographs (Fig. 1) and assistance in a variety of ways, and to Mr. A. J. Foxton for assistance with laboratory apparatus.

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3.—The Enchytraeidae (Oligochaeta) of South Western Australia: The Genus *Fridericia* Michaelsen 1889.

by J. A. Springett *

Manuscript received 17 February, 1970; accepted 28 July, 1970

Abstract

Three new species of Enchytraeidae, *Fridericia giniata* F. *holmesa* and *F. cylindrica*, are described. Two previously described species, *F. bulbosa* and *F. bulboides*, are recorded from Australia for the first time.

Introduction

Enchytraeid worms have been collected from some forest soils in the south west of Western Australia. Several of the worms belong to the genus *Fridericia* Michaelsen 1889. The genus was established in 1889 when Michaelsen discovered that certain species then assigned to *Enchytraeus*, and *Neoenchytraeus*, had definite characters in common which were of sufficient importance to justify the establishment of a new genus.

The only previous record of the genus in Western Australia is that of *F. galba* (Hoffmeister) collected by Michaelsen (1907) in Albany. The worm is common in Europe; in Albany it was found only in gardens and plant pots and Michaelsen (loc. cit.) concludes that it was introduced.

Sample sites and methods

Worms were hand-sorted from soil cores taken from the following sample sites in August, 1969 and identified using the techniques described by Nielsen and Christensen, 1959.

- Site 1 Forests Department *Pinus pinaster* plantation Gleneagle, Lat. 32° 17' S., long. 116° 8' E.
- Site 2 C.S.I.R.O. experimental apple orchard Bedfordale, Lat. 32° 12' S., long. 116° 8' E.
- Site 3 The banks of Beedelup Brook approximately 50m below Beedelup Falls, Lat. 34° 25' S., long. 115° 51' E.
- Site 4 Mixed Jarrah Forest adjacent to orchards near Donnybrook, Lat. 33° 40' S., long. 115° 52' E.

Descriptions of New Species

Fridericia giniata n.sp. (Figs. 1, 2).

A medium sized grey-white worm 15-20mm long with 59-76 segments. Cutaneous glands arranged in 4-7 rows per segment but only 1 or 2 of these distinct. Clitellum extends over XII- $\frac{1}{2}$ XIII, the glands not arranged in regular rows. Setal bundles contain 2 setae with a distinct ental hook, maximum length of setae 50 μ . Numbers of loose setae in the coelom. Peptonephridia long with two or three branches in V and two or three terminal branches in VII.

Dorsal pores present from VII. Dorsal blood vessel arises in XVII to XIX. Seminal vesicle not developed and the sperm funnel twice as long as broad. Spermathecae large, the ampulla being about 130 μ in diameter. No diverticula and the ental ducts open separately into the lateral part of the oesophagus in segment V. Ectal duct of medium length with no glands at the ectal orifice. Efferent duct of the nephridium almost terminal.

Chromosome number—32.

Material examined: About 150 specimens, of which 98 were mature.

Distribution: Sites 1 and 2. Holotype and paratype collected from site 2—Bedfordale, Lat. 32° 12' S., long. 116° 8' E. Holotype and paratype specimens deposited in the West Australian Museum (5-69, 6-69).

Discussion.—Of the previously described bisetose *Fridericia* species with no spermathecal diverticula, this species is most easily confused with *F. bulbosa* (Rosa 1887) Nielsen and Christensen 1959. *F. giniata* is a larger species both in actual length and in the number of segments. The spermathecae differ from those of *F. bulbosa* in having no glands at the ectal orifice and are more nearly like those of *F. callosa* (Eisen 1878) Nielsen and Christensen 1959. The larger size of *F. giniata*, the smaller number of setae, the presence of detached setae, the absence of a seminal vesicle and the long peptonephridia with few branches distinguish it from *F. callosa*.

Other species with which *F. giniata* shows some affinities are *F. bollonsi* Benham 1914, recorded from the Kermadec Islands, *F. parva* Moore 1895, recorded "in fallen leaves" from Philadelphia, U.S.A. and *F. alba* Moore 1895, recorded "in wet moss" from Philadelphia, U.S.A. *F. giniata* differs from *F. bollonsi* in size and number of segments, the length and shape of the peptonephridia and the absence of a seminal vesicle, and from *F. parva* in size, the number of segments, the number of setae, the shape of the peptonephridia and the absence of glands at the ectal orifice of the spermathecal duct. *F. giniata* and *F. alba* differ in the number of setae and the type of peptonephridia. These three species have a smaller spermathecal ampulla than *F. giniata*.

Fridericia cylindrica n.sp. (Fig. 3).

A medium sized species 10-15 mm long with 46-50 segments, grey-white in colour. Cutaneous glands in 1-5 rows per segment, very indistinct even in orcein stained specimens. Clitellum extends over XII-XIII, the glands not arranged

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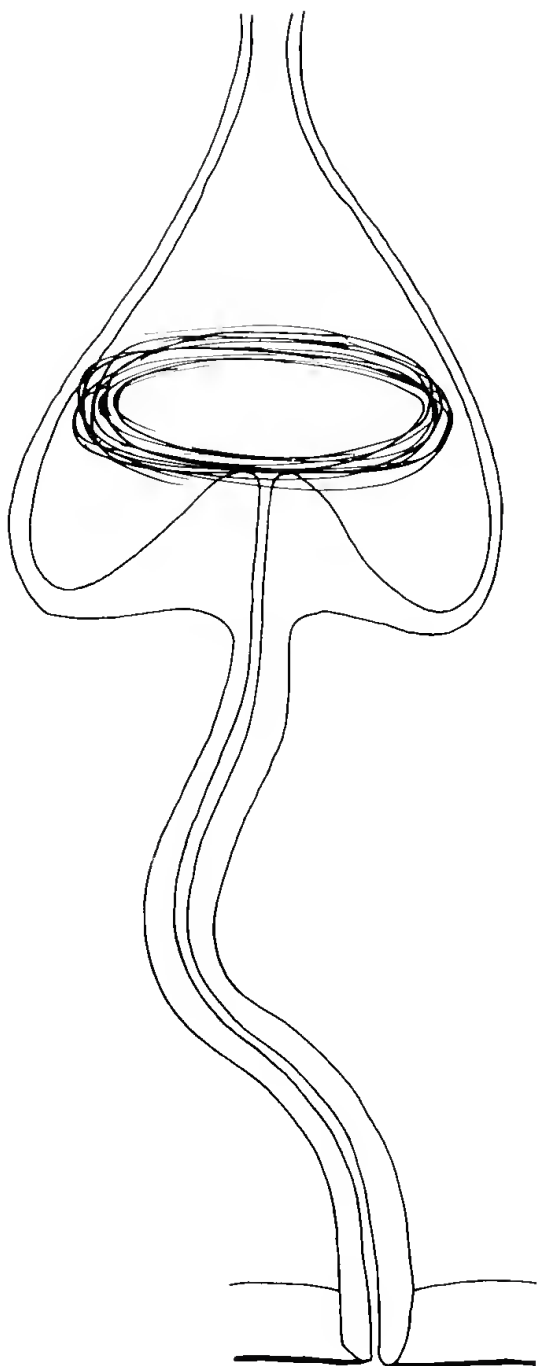


Figure 1—*Fridericia giniata* sp. nov.—spermatheca.

in rows. Setal bundles contain 2 distinctly hooked setae. Numerous detached setae in the coelom. Peptonephridia long, not coiled, with 2-4 terminal branches, sometimes extending as far back as segment VII. Dorsal vessel arises in XVII. Dorsal pores present from VII. Seminal vesicle present and well developed. Sperm funnel large, three to five times longer than broad, with a thick collar. Ectal duct of the nephridium medial. Spermatheca has two globular diverticula opening into a cylindrical ampulla. Ectal ducts the same diameter as the ampullae, having separate wide openings into the lateral part of the oesophagus. One large stalked gland at the ectal orifice.

Chromosome number—unknown.

Material examined: 57 specimens of which 43 were mature.

Distribution.—Holotype and paratype collected from Site 3—Beedelup Brook, Lat. 34° 25' S., long. 115° 51' E. Holotype and paratype specimens deposited in the West Australian Museum (7-69, 8-69).

Discussion.—Of the small bisetose *Fridericia* species with two diverticula, *Fridericia cylindrica* can be most easily confused with *F. paroniana* Issel 1904. However, the shape of the spermatheca differs; in *F. cylindrica* the ectal duct is short and stout and the ectal gland is large, projecting into the coelom for a distance of about 30 μ . The sperm funnels in *F. cylindrica* are unusual for the genus, being very long, 3-5 times longer than broad; in this character it resembles *F. regularis* Nielsen and Christensen 1959.

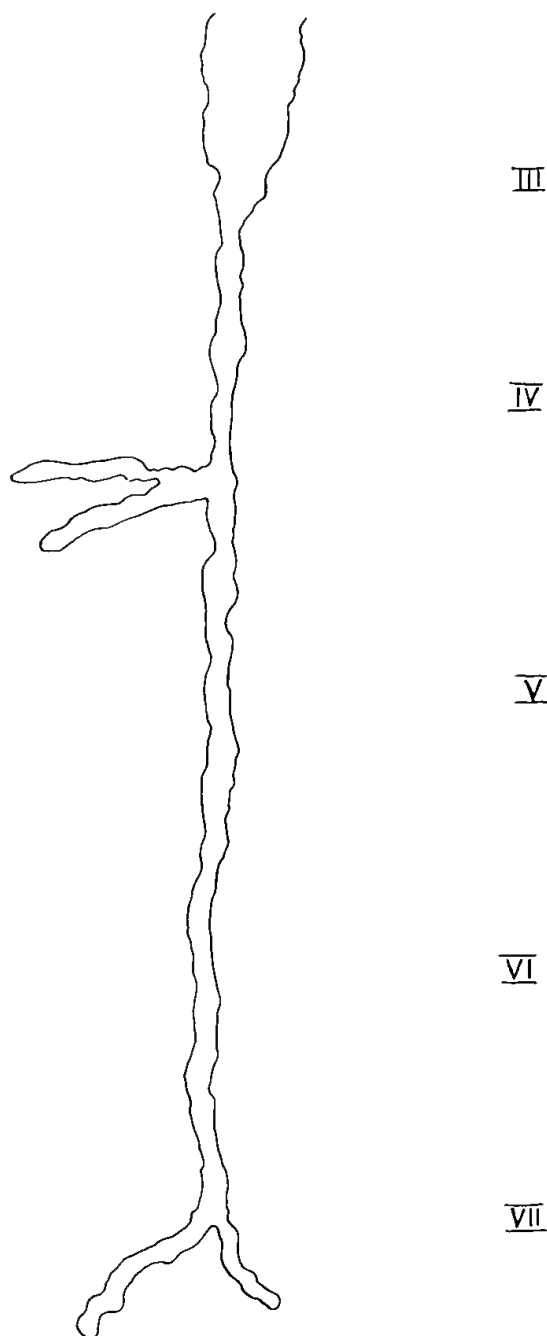


Figure 2—*Fridericia giniata* sp. nov.—peptonephridium.



Figure 3—*Fridericia cylindrica* sp. nov.—spermatheca.

Fridericia holmesa n.sp. (Figs. 4 and 5).

A medium sized worm, 10-15 mm long with 30-38 segments. Cutaneous glands in 3-5 indistinct rows per segment. Clitellum extending over XII- $\frac{1}{2}$ XIII, the glands not arranged in rows. Setal bundles containing two slightly hooked setae. Numerous packets of detached setae in the coelom. Peptonephridia long with 3-5 sub terminal branches, forming a conspicuous mass in segment IV or V. Dorsal vessel arising in segment XVII-XXII. Dorsal pores present from segment VI. Seminal vesicle present but not developed to such an extent that segments X-XI are distinctly red or brown. Sperm funnel 2-3 times longer than wide. Spermathecae with 2 diverticula and one, sometimes 2, small glands at the ectal orifice. The ental ducts merge and there is one opening into the mid dorsal part of the oesophagus at VI/VII.

Chromosome number—unknown.

Material examined: 62 specimens, all of which were mature.

Distribution.—Holotype and paratype from Site 3—Beedelup Brook, Lat. 34° 25' S., long. 115° 51' E. Holotype and paratype specimens are deposited in the West Australian Museum (7-69, 8-69).

Discussion

The ten species listed below have been described as having one spermathecal opening into the oesophagus.

<i>F. connata</i>	Bretscher 1902
<i>F. baskini</i>	Cernovitov 1937 augm. Nielsen and Christensen 1959
<i>F. gamotheca</i>	Issel 1904
<i>F. caprensis</i>	Bell 1947
<i>F. pretoriana</i>	Stephenson 1930
<i>F. berkeleyensis</i>	Bell 1936
<i>F. losangelensis</i>	Bell 1936
<i>F. variata</i>	Bretscher 1902
<i>F. bulboides</i>	Nielsen and Christensen 1959.

Of these species *F. caprensis*, *F. pretoriana*, *F. berkeleyensis*, *F. losangelensis*, *F. bulboides* and *F. variata* have no diverticula, *F. uniampullata* has a total of 7-9 diverticula and in *F. gamothecae* the ampullae are described as completely united into a spherical sac.

In *F. baskini* there are 4-7 preclitellar setae. *F. connata* is most similar to *F. holmesa* but can be distinguished from it by (1) the arrangement of the cutaneous and clitellar gland cells, distinct and regular in *F. connata*, indistinct and irregular in *F. holmesa*; (2) the peptonephridia which are very long in *F. holmesa* and are curled round to form a dense mass in segment IV or V; (3) the spermatheca which are of similar construction, but in *F. holmesa* only the ental ducts unite, not the ampullae, the opening into the oesophagus being in the rear part of segment VI. The gland at the ectal orifice is fairly large and in some specimens a second gland has been noted.

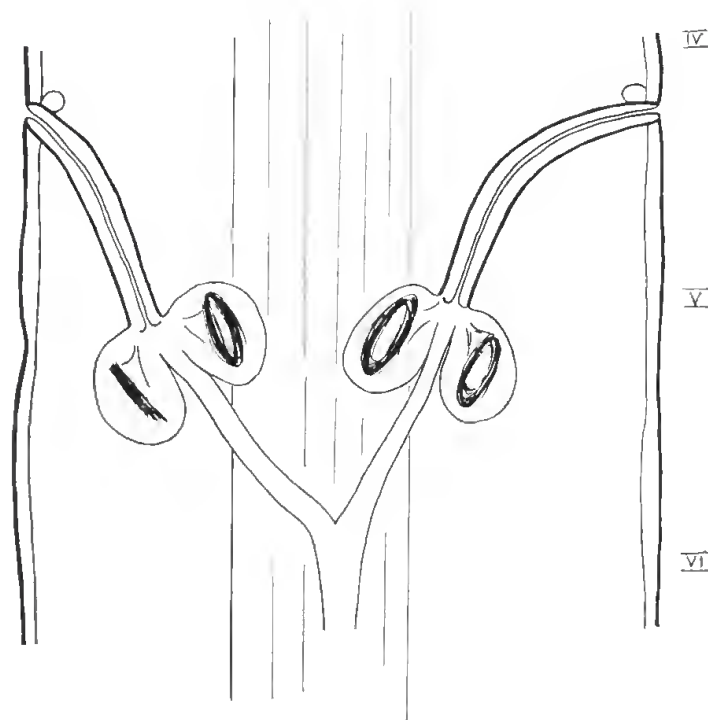


Figure 4—*Fridericia holmesa* sp. nov.—spermathecae.

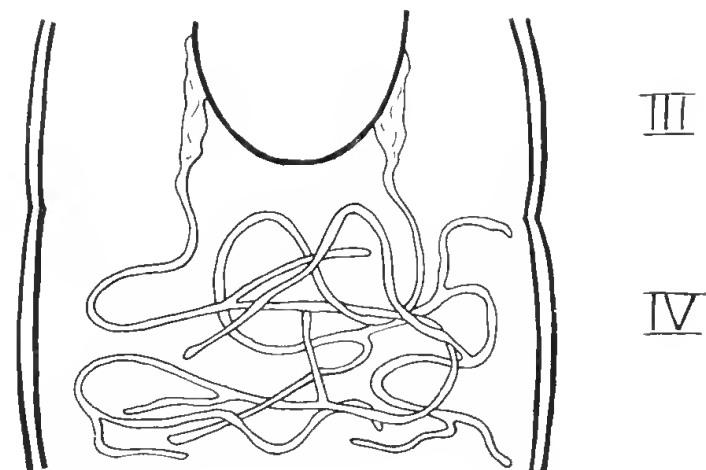


Figure 5—*Fridericia holmesa* sp. nov.—peptonephridia.

New Australian Records

Fridericia bulbosa (Rosa) 1887 Nielsen and Christensen 1959.

A small bisetose worm, 8-10 mm long with 22-27 segments and a chromosome number of 32, was found at site 4. Thirty-five mature specimens were examined. The structure is identical with that of the Danish specimens described by Nielsen and Christensen 1959. The known distribution of this species is:

Italy	(Rosa 1887, and Nielsen and Christensen 1963)
Armenia	(Cernosvitov 1941)
Denmark	(Nielsen and Christensen 1959)
Iceland	(Christensen 1962)
Norway	(Abrahamsen 1968)
Western Australia	(Springett).

Specimens are deposited in the Western Australian State Museum (11-69).

Fridericia bulboides Nielsen and Christensen 1959.

Specimens of this species 8-12 mm long with 28-32 segments were also found at site 4. Twenty-eight mature specimens were examined. The species is essentially the same as that described by Nielsen and Christensen, having the characteristic peptonephridia with either a dense coil near the ectal duct of the spermatheca or a loop projecting forward into segment IV; in some specimens both loop and coil were present. The specimens found in Western Australia differ from the Danish specimens in having a fairly large, easily visible sessile gland at the ectal orifice of the spermathecal duct and in having no loose setae in the coelom. The chromosome number of the Australian specimens is unknown. The known distribution of the species is:

Denmark	(Nielsen and Christensen 1959)
Sweden	(Nielsen and Christensen 1961)
Iceland	(Christensen 1962)
Finland	(Nurminen 1965)
Norway	(Abrahamsen 1968)
Western Australia	(Springett).

Specimens are deposited in the Western Australian State Museum (12-69).

General discussion

Of the six species of *Fridericia* recorded in Western Australia three are new to science and three have a European distribution. As all the *Fridericia* recorded have been found in or near agricultural areas, and the enchytraeid fauna of the European Mediterranean area is largely undescribed, it is not possible to say whether *F. giniata*, *F. holmesa* and *F. cylindrica* are endemic.

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4.—Skull and tooth variation in Australian bandicoots (Peramelidae, Marsupialia): the genus *Isoodon* and multivariate comparisons with *Perameles*

by L. Freedman* and G. P. Rightmire

Manuscript received 18 August 1970; accepted 17 November 1970.

Abstract

The morphological and metrical features of the skull and teeth of certain taxa of the genus *Isoodon* are described and analysed. Multivariate comparisons are then made between these and a number of *Perameles* taxa. The main multiple discriminant analyses, using either cranial or dental features alone, achieve good separation of the genera (principally on the 1st function), and of the lower taxa within each genus (mainly by the 2nd function).

Introduction

This study is part of an ongoing investigation being made of skull and tooth variation in the bandicoots (Peramelidae: Marsupialia) of Australia. In a series of previous studies (Freedman, 1967; Freedman and Joffe 1967a and b), the anatomical and metrical features of the skull and teeth of species of the genus *Perameles*, the long-nosed bandicoots, were reported on. The present study utilises material from the major United States collections to examine the variations of the same features in certain species of the genus *Isoodon*, the short-nosed bandicoots. The main sample is of *I. macrourus*. In addition multivariate comparisons are made of the cranial and dental features of a number of taxa of *Isoodon* and *Perameles*. The usefulness of multivariate discriminant analysis in taxonomic studies is again apparent.

Taxonomy of *Isoodon*

In most of the recent classifications of the genus *Isoodon* nine taxa are recognised. Thus, Tate (1948) and Marlow (1962) both list three species in the genus, the first two species each including a number of subspecies. The species they list are: *I. obesulus* (with 6 subspecies), *I. macrourus* (with 2 subspecies) and *I. barrowensis* (monotypic). For the same genus, Troughton (1957) delimits nine similar groups, but he describes *I. obesulus* as comprised of 3 subspecies and he regards the remaining 6 taxa as each being of full specific rank.

In the present study, a classification and distribution ranges similar to those outlined by Tate (1948) and Marlow (1962) will be used (Fig. 1). Thus, *I. obesulus* includes *I. o. obesulus* (southern half of coastal New South Wales, most of Victoria and an adjacent coastal portion of South Australia), *I. o. affinis* (Tasmania), *I. o. nauticus* (2 islands in the Nuyts Archipelago off the coast of South Australia), *I. o. fusciventer* (south west part of Western Australia), *I. o.*

auratus (north east part of Western Australia and adjacent Northern Territory) and *I. o. peninsulae* (northern tip of Queensland). The species *I. macrourus* includes *I. m. macrourus* (northern part of Northern Territory) and *I. m. torosus* (east coast of Queensland and north half of the coast of New South Wales). The third species is *I. barrowensis* and its locality is Barrow Island, off the north west coast of Western Australia.

Materials and Methods

The samples of the genus *Isoodon* assembled for the present study total 77 individuals and are from collections in the United States of America. They were kindly made available to us by the American Museum of Natural History and the Archbold Expeditions, New York (Dr. Hobart M. van Deusen), the Field Museum of Natural History, Chicago (Dr. William D. Turnbull) and the Smithsonian Institution, Washington (Dr. Henry W. Setzer). This material includes 24 specimens of *I. m. macrourus* (15 males and 9 females) and 38 specimens of *I. m. torosus* (24 males and 14 females). The sexes of a few of the *I. m. torosus* individuals were not recorded, and (on criteria discussed below) they were sexed on morphology and size. The number of *I. obesulus* specimens is only 14, and of these there are only 6 known males and 3 known females. The sample of this species includes individuals of *I. o. obesulus*, *I. o. affinis*, and *I. o. fusciventer*, but, because of the very small numbers, no attempt was made to treat these subspecies separately. Of *I. barrowensis* there is only a single specimen (Smithsonian Institution No. 218462). The whole of the available sample has been utilized for the morphological description and univariate analysis of *Isoodon*.

The main multivariate statistical tool used for comparing taxa was discriminant function analysis. Various aspects of the principles and methodology of the technique will be dealt with in the course of describing and discussing comparisons and results. Computation of the discriminants here reported was carried out at the University of Wisconsin Computer Center using a slightly modified version of program EIDISC (distributed by the Vogelback Computing Center, Northwestern University). This program provides output similar to that discussed in chapters 6 and 7 of Cooley and Lohnes (1962).

For the multivariate analyses utilizing the *Isoodon* data, the numbers in the various taxa had to be slightly reduced (Table 8) due to cer-

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tain of the specimens being either immature or damaged. The *Perameles* samples used in those tests (175 individuals) were described in Freedman (1967). The measurements, aging and sexing criteria, and the general methodology utilised in the present study, are outlined in Freedman and Joffe (1967a).

Skull and dental morphology in *Isoodon*

A fairly detailed morphological description, including drawings and photographs, was given by Freedman (1967) of the skull and dental features of *Perameles nasuta*. In that same study, the morphological variations of *P. gunnii* and *P. bougainville* from the *P. nasuta* description were also outlined, and standard view photographs of these two species were included in that and two subsequent papers (Freedman and Joffe, 1967a and b). The basic *P. nasuta* description very largely also holds for the genus *Isoodon* and, in the present study, only a series of standard view photographs and brief notes highlighting the important differences of the various *Isoodon* taxa to the *P. nasuta* description will be given.

(a) *I. macrourus*.—The skull of *I. macrourus* (Fig 2, *I. m. macrourus*) is very much more robustly constructed in all respects than that of *P. nasuta*. The bone is generally thicker and the muscle markings are far more prominent. The length of the *I. m. torosus* cranium is, on average, almost as great as that of *P. nasuta*, but the

mean cranial length of *I. m. macrourus* is rather less than in that species, the decrease in the females being less marked than in the males.

Compared to *P. nasuta*, the cranial breadth and height dimensions appear to be absolutely greater in *I. m. torosus*, but only relatively greater in *I. m. macrourus*. Notable amongst the differences in overall shape of the cranium is the greater relative muzzle breadth in both subspecies of *I. macrourus* which makes the muzzle appear relatively shorter and less attenuated distally than in *P. nasuta*. It is mainly this feature which gives the genus *Isoodon* its popular name of short-nosed bandicoots.

In the palate the posterior palatine vacuities of *I. macrourus* are rather smaller than those in *P. nasuta* and the premaxillae do not project anteriorly as far beyond the incisors as they do in that form. Perhaps the two most marked cranial differences between *I. macrourus* and *P. nasuta* are the more heavily built zygomatic arches and, on the undersurface of the cranium, the very greatly inflated alisphenoid bullae in the former species. In the mandible of *I. macrourus* the coronoid process, and in fact the whole of the ascending ramus, is particularly broad in an antero-posterior direction. Also, the ramus is more nearly at right angles to the body than in *P. nasuta* and this feature is more marked in *I. m. macrourus* than in *I. m. torosus*.

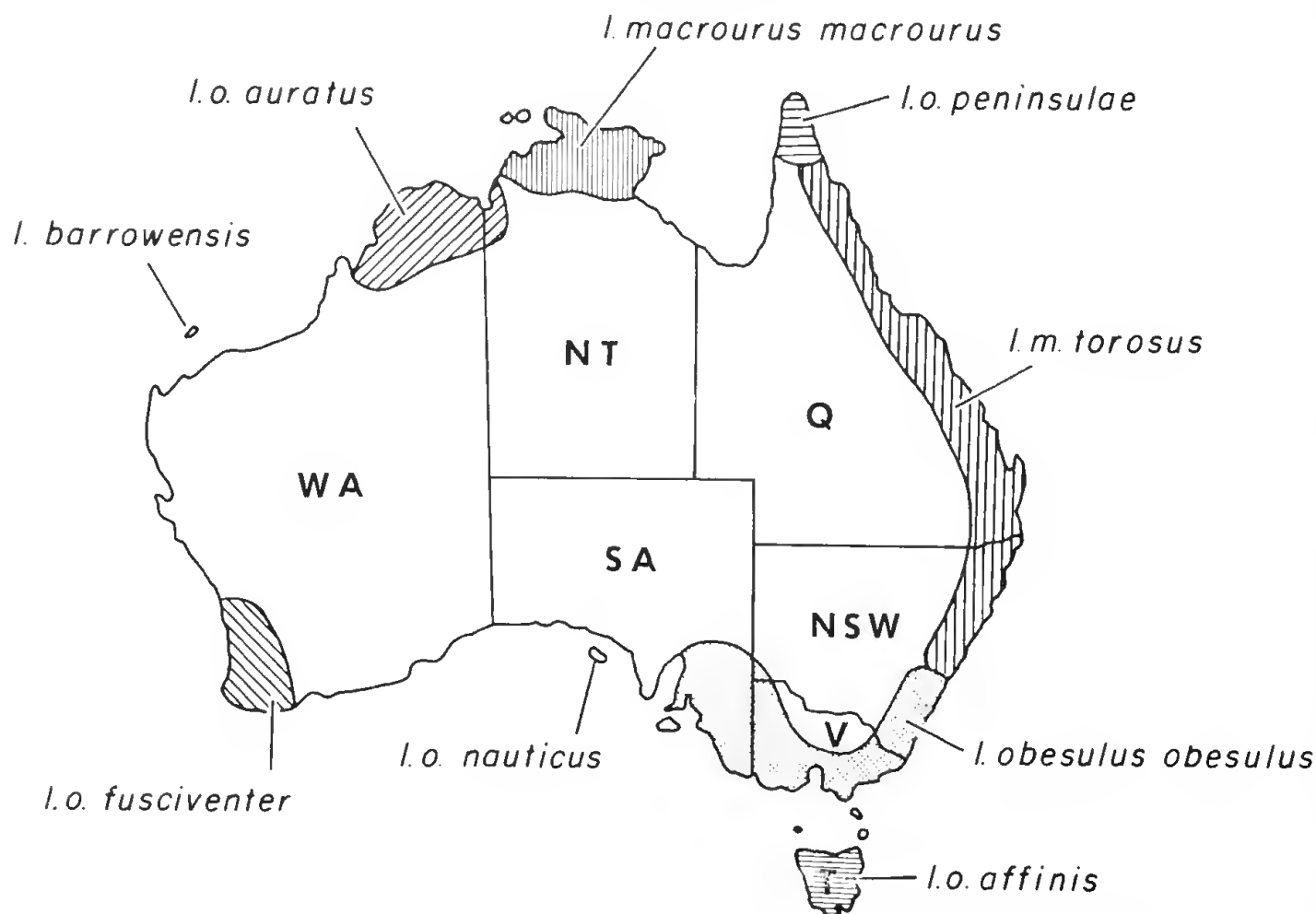


Figure 1.—Map of Australia to show the distribution of taxa of the genus *Isoodon*. (After Marlow, 1962, "Marsupials of Australia", Jacaranda Press, Brisbane).

The individual teeth of *I. macrourus* are considerably larger than those of *P. nasuta*, with the exception of I^1 which is a particularly small tooth. The molar teeth are also more square in *I. macrourus* and in the upper molars the distobuccal corner is not elongated distally as in *P. nasuta*. In addition the last premolar in *I. macrourus*, especially the upper tooth, is a particularly broad and robust tooth.

Sexual dimorphism in the skull and teeth of *I. m. torosus* appears to be restricted to size differences in most of the skull dimensions and tooth row lengths, the canine tooth dimensions and, of the single other teeth, mainly in measurements of M4. The morphological sex difference in the canine teeth described in *Perameles* species does not appear to be consistently present in *Isoodon*. In *I. m. macrourus*, except in canine size, there was little evidence of sexual dimorphism in the skull or teeth.

(b) *I. obesulus*.—In the other species of *Isoodon* for which a fair sample is available, *I. obesulus*, the skulls are considerably smaller than in *P. nasuta* and rather more similar in size to *P. bougainville*. The male individual shown in Figure 3 (*I. o. affinis*) is the largest specimen of

I. obesulus measured. Although very much smaller in size, the overall shape of *I. obesulus* is very similar to that of *I. macrourus* and it also shows the very greatly inflated bullae characteristic of the genus *Isoodon*.

In the structure of the palate, *I. obesulus* is different to *P. nasuta* and also to *I. macrourus*, but shows resemblance to both *P. gunnii* and *P. bougainville*. As in those species, between the anterior and posterior palatine vacuities there is an additional pair of fairly large antero-posteriorly elongated vacuities, and posterior to the posterior pair, which are large, there is a scattered group of vacuities lying close to the posterior end of the palate. In the mandible, the angle of the ascending ramus to the body is more obtuse than in *I. macrourus*, however, the ramus is antero-posteriorly broad as in that species.

In the dentition, the molars of *I. obesulus*, like those of *I. macrourus*, appear more compact than those of *P. nasuta*, and, especially in the upper jaw, the teeth show evidence of being more crowded than in either *P. nasuta* or *I. macrourus*. P^3 is similar to the equivalent tooth

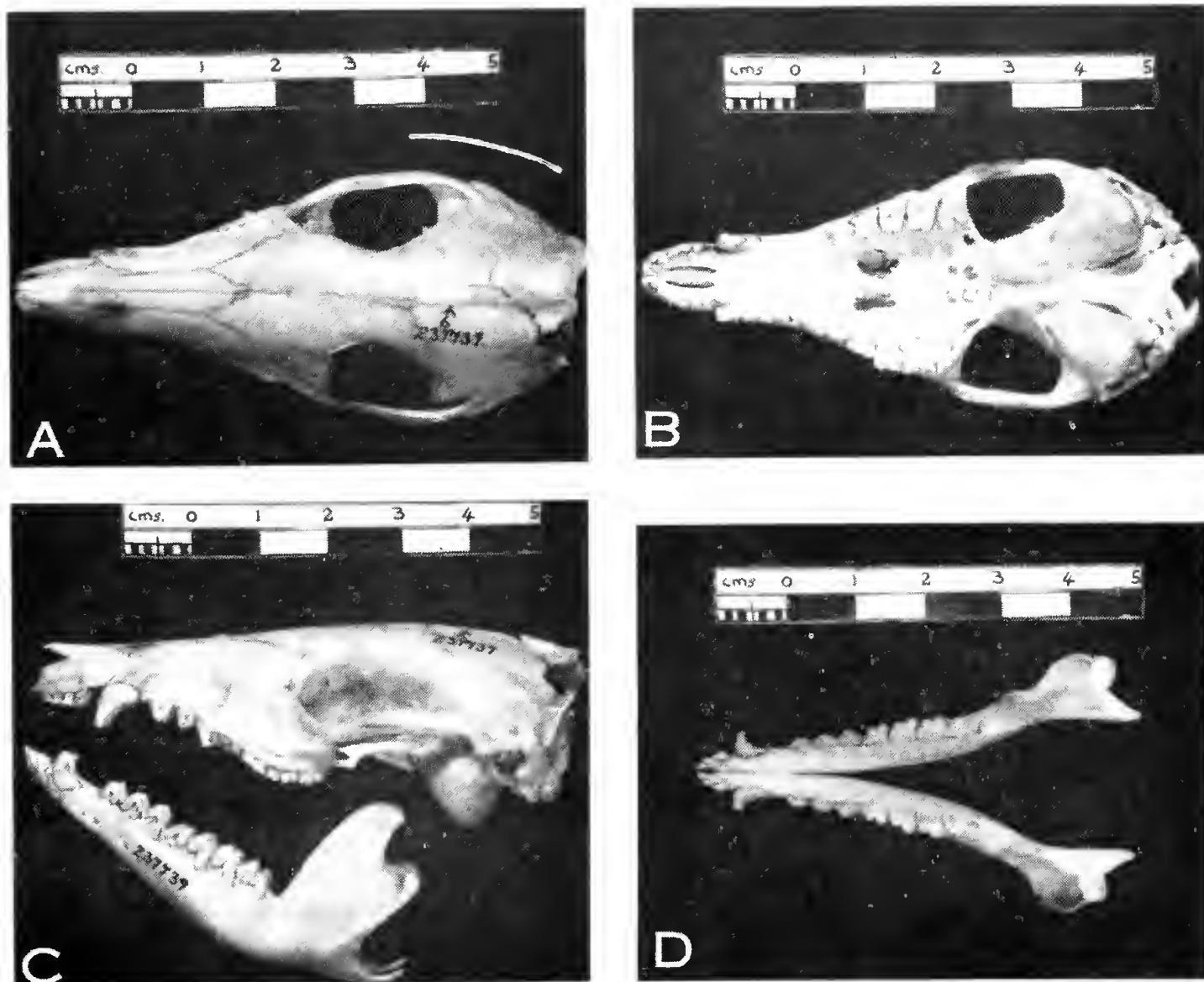


Figure 2.—*Isoodon macrourus macrourus* male (Smithsonian Inst. No. 237739). A.—dorsal view of cranium; B.—ventral view of cranium; C.—lateral view of cranium and mandible; D.—occlusal view of mandible.

TABLE 1

Comparison of *Isoodon m. torosus* male and female skull measurements (in mm)

Measurement	Males			Females			"t"
	N	\bar{X}	VAR.	N	\bar{X}	VAR.	
Cranium—							
(a) length—							
Max.	18	84.74	42.24	7	74.62	18.34	3.786**
Bas.	18	75.92	25.81	7	67.72	12.37	3.897**
Cond.-Bas.	18	79.78	26.06	7	70.98	16.27	4.074**
Pal.	18	49.71	11.05	8	45.03	7.19	3.496**
Nas.	18	33.88	10.69	6	31.11	6.61	1.880n.s.
Fr.	18	25.64	7.17	7	21.55	2.01	3.804**
Par.	18	22.16	5.68	7	19.72	2.83	2.465*
Ant. to P ¹	16	2.13	0.05	7	1.98	0.02	1.626n.s.
(b) breadth							
Ant. to C	18	9.42	0.49	8	8.03	0.31	4.945**
at M ²	18	23.76	2.35	8	21.47	1.09	3.827**
Int.-Orb.	18	22.66	2.32	8	20.21	0.40	4.346**
Min. Fr.	18	11.81	0.30	7	11.65	0.20	0.686n.s.
Bizyg.	18	37.31	7.15	7	31.94	2.72	4.924**
Cran.	18	27.34	3.09	7	24.65	1.75	3.648**
(c) height—							
Ant. to C	17	7.35	0.34	8	6.15	0.12	5.356**
Post. to M ¹	18	20.37	1.11	8	18.23	0.40	5.300**
Cran.	18	27.83	2.21	7	25.32	0.93	4.113**
Occip.	18	21.37	2.74	7	18.57	0.20	4.361**
(d) bulla—							
L	18	12.20	1.61	7	10.64	0.20	3.142**
B	18	8.83	0.28	7	8.37	0.09	2.151*
(e) vacuities							
A.P. vac.							
L	17	6.39	0.72	7	6.34	0.35	0.141n.s.
P.P. vac.							
L	17	6.81	0.58	8	6.46	0.76	1.024n.s.
B	18	9.75	1.00	8	9.16	0.91	1.407n.s.
Mandible—							
Max. L.	17	64.47	20.75	8	57.03	13.58	4.027**
Ramus L.	18	14.52	2.00	8	12.03	1.41	4.334**
Br. at M ₂	18	4.81	0.19	8	3.91	0.13	5.099**
Ht. at M ₂	18	7.56	0.62	8	6.41	0.39	3.639**
Ramus Angle	18	74.38	11.19	8	77.87	3.26	2.756*

Significance levels :

t-Test : ** = 1%; * = 5%; n.s. = not significant.

1% level. On the other hand, the corresponding numbers of significant differences between the sexes in *I. m. macrourus* (Tables 4-6) are very small (cranial: 3/28; upper teeth 5/26; lower teeth: 6/25).

TABLE 2

Comparison of *Isoodon m. torosus* male and female upper tooth measurements (in mm)

Measurement	Males			Females			"t"
	N	\bar{X}	VAR.	N	\bar{X}	VAR.	
P ¹ -M ¹	17	45.20	5.37	8	41.35	6.50	3.756**
P ¹ -P ²	17	6.45	0.20	10	6.01	0.10	2.726*
C-M ¹	19	34.30	4.99	8	31.08	3.44	3.579**
M ¹ -M ²	20	17.19	0.93	8	15.97	0.71	3.125**
P ² -L	24	1.68	0.03	12	1.50	0.02	3.111**
C-L	19	4.20	0.56	10	2.35	0.11	7.395**
B	19	2.12	0.09	10	1.32	0.02	7.930**
H	19	6.44	1.99	8	3.56	0.29	5.553**
P ¹ -L	24	2.81	0.04	13	2.80	0.04	0.145n.s.
B	24	1.30	0.01	13	1.25	0.01	1.451n.s.
P ² -L	24	2.95	0.02	13	3.04	0.009	2.051*
B	25	1.68	0.009	12	1.60	0.04	1.663n.s.
P ² -L	22	3.71	0.13	8	3.35	0.04	2.659*
B	22	2.80	0.03	8	2.65	0.04	2.015n.s.
M ¹ -B	25	3.73	0.03	14	3.65	0.06	1.190n.s.
LB	25	4.25	0.06	14	4.22	0.05	0.378n.s.
LL	24	3.19	0.08	14	3.15	0.06	0.440n.s.
M ² -B	25	4.36	0.11	14	4.27	0.10	0.826n.s.
LB	25	4.26	0.06	14	4.23	0.03	0.404n.s.
LL	25	3.50	0.07	14	3.50	0.08	0.000n.s.
M ² -B	24	4.77	0.16	9	4.75	0.17	0.126n.s.
LB	24	4.91	0.11	9	4.65	0.14	1.938n.s.
LL	24	4.02	0.07	9	3.74	0.09	2.612**
M ³ -B	20	3.74	0.06	8	3.46	0.02	3.016**
LB	20	4.82	0.08	8	4.17	0.06	5.688**
LL	19	2.40	0.05	8	2.17	0.04	2.511*

Significance levels :

t-Test : ** = 1%; * = 5%; n.s. = not significant.

TABLE 3

Comparison of *Isoodon m. torosus* male and female lower tooth measurement (in mm)

Measurement	Males			Females			"t"
	N	\bar{X}	VAR.	N	\bar{X}	VAR.	
I ₁ -M ₁	16	43.02	6.21	9	40.04	6.86	2.819**
I ₁ -I ₃	19	5.20	0.29	12	5.13	0.13	0.396n.s.
C-M ₁	20	36.06	6.46	9	32.90	4.80	3.222**
M ₁ -M ₁	22	18.32	0.77	9	17.42	0.78	2.587*
C-L	19	3.60	0.44	9	2.34	0.13	5.304**
B	19	2.00	0.08	9	1.26	0.01	7.563**
H	18	4.95	0.95	8	2.70	0.18	6.217**
P ₁ -L	24	2.99	0.72	14	2.08	0.04	0.043n.s.
B	24	1.13	0.004	14	1.08	0.003	2.464*
P ₂ -L	24	3.16	0.03	14	3.15	0.02	0.183n.s.
B	24	1.44	0.01	14	1.33	0.01	3.270**
P ₃ -L	21	3.60	0.08	9	3.45	0.02	1.501n.s.
B	22	2.01	0.02	9	1.91	0.02	1.787n.s.
M ₁ -BM	22	2.53	0.02	14	2.40	0.04	2.280*
BD	22	3.01	0.03	14	2.86	0.07	2.061*
L	23	3.91	0.06	14	3.73	0.07	2.103*
M ₂ -BM	25	3.02	0.02	14	2.96	0.07	0.927n.s.
BD	25	3.53	0.07	14	3.27	0.13	2.580*
L	25	4.28	0.08	14	4.29	0.06	0.110n.s.
M ₃ -BM	25	3.32	0.04	14	3.22	0.06	1.381n.s.
BD	25	3.44	0.08	13	3.30	0.09	1.418n.s.
L	25	4.61	0.09	13	4.60	0.08	0.099n.s.
M ₄ -BM	22	3.14	0.03	9	3.07	0.05	0.938n.s.
BD	22	2.55	0.04	9	2.18	0.02	5.035**
L	22	5.55	0.07	9	5.14	0.02	4.370**

Significance levels :

t-Test : ** = 1%; * = 5%; n.s. = not significant.

available specimens adequate for subspecific separation. Thus, and because of the overall small number of specimens, the only statistics of *I. obesulus* included in the present paper (Table 7) are the combined male and female mean values and variances for the species as a whole (as enumerated in Materials and Methods above) for the various dimensions used in the discriminant analysis.

Comparisons of the figures in these seven tables with those in the previous papers on *Perameles* (Freedman, 1967 and Freedman and Joffe, 1967a and b), confirm the various size interrelationships already noted above in the morphological comparisons. Numerous other differences for particular dimensions also become apparent. Those related to sexual dimorphism are dealt with below; others will be discussed later in the course of analysing the discriminant functions.

With regard to sexual dimorphism in the metrical features studied, the "t" values included in Tables 1-3 indicate that, in *I. m. torosus*, for the majority of the cranial dimensions (22/28) and for over half of the dental measurements (upper teeth: 14/26; lower teeth: 14/25) the differences are significant at the 5% level, and in most of these instances significance is actually at the

in *I. macrourus* and so are the very small I¹ teeth. In the small sample available sexual dimorphism was not detected.

(c) *I. barrowensis*:—The single male *I. barrowensis* individual is very similar to the *I. obesulus* specimens in morphology, but, on size, it appeared to be slightly smaller. Because only this one specimen is currently available, no further comments on the morphology seem appropriate.

In a recent paper analysing fossil bandicoots from Mammoth Cave, Western Australia, Merri-
 lees (1967) has listed a series of features useful for distinguishing the genera *Macrotis*, *Isoodon*, *Perameles* and *Chaeropus*. With regard to *Isoodon* and *Perameles*, the present study confirms and extends the shape differences in the muzzle, mandible and molar teeth listed by Merri-
 lees and also describes certain other important differences. The only point of major disagreement between the two studies relates to the alisphenoid bulla. Merri-
 lees describes these as being large in both *Isoodon* and *Perameles*, although differing in shape. As stated in ships differ in the two sexes and these are not treated separately in the table. In the same

the text and illustrated in photographs in 2 previous studies (Freedman, 1967; Freedman and Joffe, 1967b) the bulla is relatively small in *P. nasuta*, *P. gunnii* and *P. b. bougainville* and only of comparable relative size to that of *Isoodon* in *P. b. notina*. The relationship difference between the first premolar and the adjacent canine tooth, which this author discusses, is difficult to evaluate, mainly because the relation-
 paper, Merri-
 lees gives a most useful table of tooth alveoli dimensions for the 4 bandicoot genera. These will not be discussed below as they are not strictly comparable to the actual tooth dimensions recorded in the present study.

Analysis of *Isoodon* metrical features

Univariate comparisons

The means and variances, in the males and females separately, for the cranial and dental features studied in *I. m. torosus* and *I. m. macrourus* are listed in Tables 1-6. Study of the individual measurements in the males and females of *I. obesulus* did not indicate any obvious sexual dimorphism in the features which were to be used for the discriminant analysis. Nor, as pointed out above, were the numbers of the

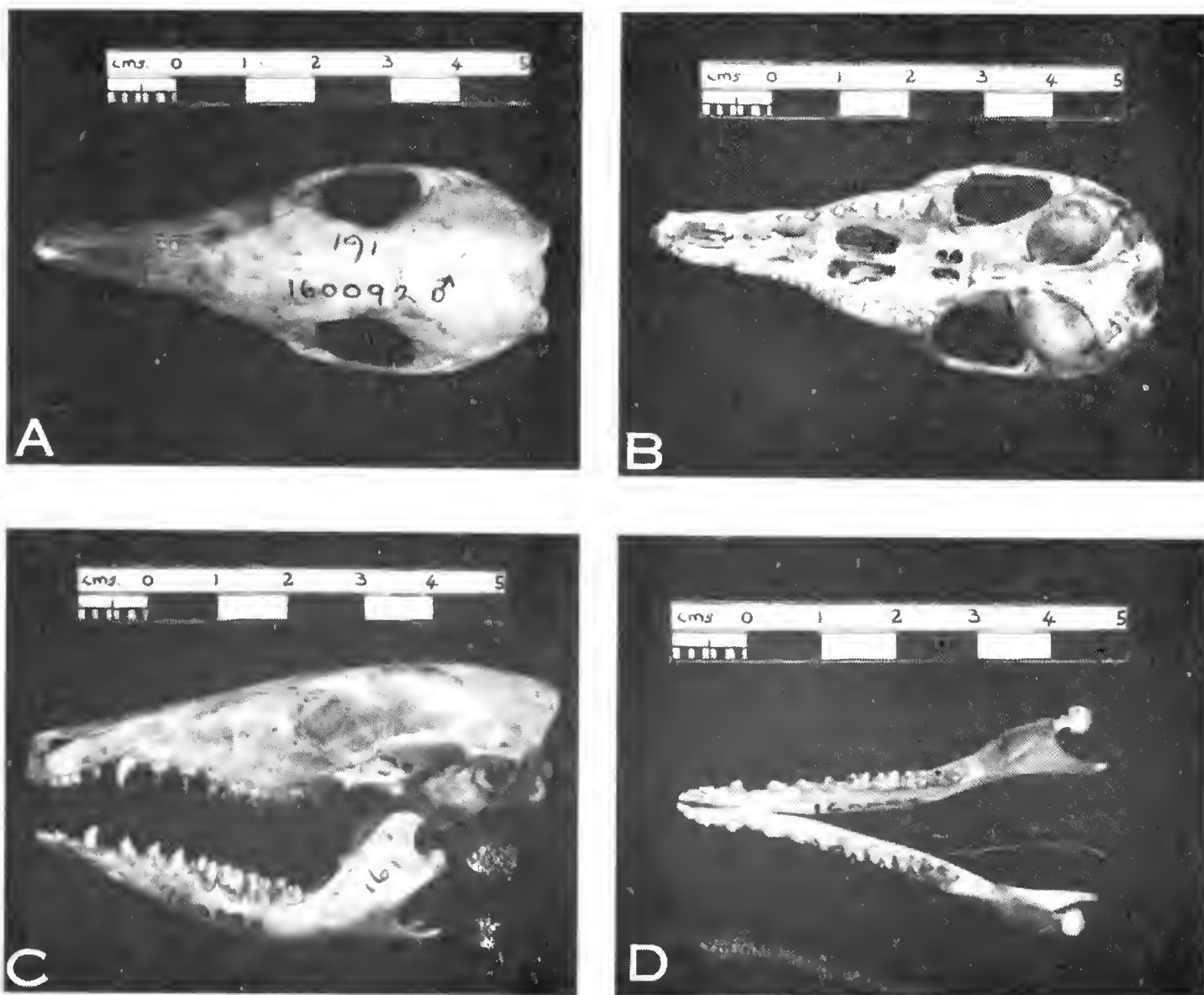


Figure 3. *Isoodon obesulus affinis* male (Amer. Mus. Nat. Hist. No. 160092). A.—dorsal view of cranium; B.—ventral view of cranium; C.—lateral view of cranium and mandible; D.—occlusal view of mandible.

TABLE 4

Comparison of *Isaodon m. macrourus* male and female skull measurements (in mm)

Measurement	Males			Females			t
	N	\bar{X}	VAR.	N	\bar{X}	VAR.	
Cranium							
(a) length							
Max.	11	75.86	30.24	4	70.77	3.48	1.787n.s.
Bas.	12	68.70	23.00	4	65.12	2.32	1.438n.s.
Cond.-Bas.	12	72.17	23.55	4	68.72	2.05	1.372n.s.
Pal.	12	44.40	9.02	4	42.95	1.03	0.929n.s.
Nas.	11	30.20	7.35	5	28.58	4.58	1.172n.s.
Fr.	14	23.58	2.58	4	21.92	1.36	1.009n.s.
Par.	14	19.65	4.26	4	16.95	1.80	2.443*
Ant. to P ¹	13	2.00	0.04	5	1.90	0.02	1.015n.s.
(b) breadth							
Ant. to C	13	8.56	0.69	5	7.70	0.08	2.229*
at M ²	13	21.78	2.52	5	20.36	0.12	1.947n.s.
Int.-Orb.	13	20.53	3.06	5	19.36	0.57	1.424n.s.
Min. Fr.	13	11.27	0.29	4	11.67	0.80	1.117n.s.
Bizyg.	12	33.47	6.34	4	31.25	0.30	1.711n.s.
Cran.	12	25.98	7.67	4	23.62	1.00	1.634n.s.
(c) height							
Ant. to C	13	6.26	0.40	5	5.70	0.14	1.641n.s.
Post. to M ¹	12	19.01	1.24	4	18.12	0.08	1.548n.s.
Cran.	12	25.85	3.00	4	24.52	0.61	1.440n.s.
Occip.	12	19.75	2.72	4	17.95	0.07	2.125n.s.
(d) bulla							
L	14	11.80	0.95	4	11.87	0.05	0.139n.s.
B	14	9.18	0.25	5	8.84	0.06	1.440n.s.
(e) vacuities							
A.P. vac.							
L	12	5.86	0.40	5	6.12	0.03	0.889n.s.
P.P. vac.							
L	13	5.33	0.88	5	5.68	0.21	0.787n.s.
P.P. vac.							
B	13	8.43	1.39	5	8.52	0.38	0.160n.s.
Mandible							
Max. L	13	57.00	14.98	5	54.12	2.02	1.597n.s.
Ramus L.	13	12.76	1.49	5	11.36	0.16	2.472*
Br. at M ₂	13	4.13	0.15	5	3.82	0.05	1.666n.s.
Ht. at M ₂	12	7.32	0.91	5	6.48	0.14	1.879n.s.
Ramus Angle	13	78.00	6.00	5	78.60	4.80	0.477n.s.

Significance levels :

t-Test : ** 1% ; * 5% ; n.s. not significant.

The subspecific status of *I. m. macrourus* and *I. m. torosus*

An attempt was next made to investigate the subspecific validity of *I. m. torosus* and *I. m. macrourus*. Because of the marked size sexual dimorphism found in *I. m. torosus* it was considered necessary to treat the sexes separately in investigating the two subspecies. The analysis was made by computing a discriminant function on 27 cranial features to maximise the difference between the males of the two subspecies. The computed function gave a mean score of -27.706 for *I. m. torosus* males (N=18) and -22.649 for *I. m. macrourus* males (N=13). Using a sectioning point of -25.177, 3 *I. m. torosus* males fell on the *I. m. macrourus* side of the total distribution, and 3 *I. m. macrourus* males were included on the *I. m. torosus* side.

As a measure of the subspecific validity of the two samples, this test does not meet a stringent application of the 75% rule (i.e. that a subspecies is valid if 75% of the individuals differ from all (= 97%) of a previous subspecies—Mayr, 1969, p. 190). For the discriminant function computed, if a sectioning point is drawn to include all *I. m. macrourus*, 7 out of 18 *I. m. torosus* are included in the *I. m. macrourus* section, i.e. only 61% are excluded. Done in reverse

fashion, only 2 out of 13 *I. m. macrourus* are not included in the *I. m. torosus* category. However, as this test only involves certain cranial characters, and many other sorts of features can

TABLE 5

Comparison of *Isaodon m. macrourus* male and female upper tooth measurements (in mm)

Measurement	Males			Females			t
	N	\bar{X}	VAR.	N	\bar{X}	VAR.	
P ¹ M ¹	14	40.13	3.96	5	38.88	1.56	1.302n.s.
P ¹ P ¹	14	5.63	0.08	5	5.48	0.03	1.102n.s.
C ¹ M ¹	14	31.62	2.63	6	30.03	1.23	2.176*
M ¹ M ¹	14	15.48	0.37	6	16.05	0.72	1.708n.s.
P ² L	15	1.31	0.02	8	1.28	0.01	0.530n.s.
C ¹ L	13	4.34	1.61	8	2.06	0.03	5.004**
B	14	1.90	0.10	8	1.21	0.01	5.948**
H	13	5.16	0.96	7	3.35	0.13	4.670**
P ² L	15	2.62	0.03	9	2.57	0.02	0.730n.s.
B	15	1.22	0.004	9	1.18	0.006	1.379n.s.
P ² L	15	2.62	0.04	9	2.66	0.02	0.524n.s.
B	15	1.60	0.01	9	1.58	0.03	0.360n.s.
P ³ L	13	3.30	0.14	8	3.00	0.06	2.008n.s.
B	14	2.65	0.03	8	2.68	0.02	0.415n.s.
M ¹ B	16	3.67	0.03	9	3.67	0.02	0.000n.s.
LB	16	3.84	0.03	9	3.76	0.04	1.049n.s.
LL	16	2.81	0.09	9	2.85	0.01	0.385n.s.
M ² B	15	4.38	0.18	9	4.07	0.07	1.964n.s.
LB	16	3.95	0.02	9	3.90	0.02	0.848n.s.
LL	15	3.18	0.15	9	3.13	0.03	0.363n.s.
M ³ B	14	4.82	0.26	8	4.31	0.10	2.547*
LB	14	4.30	0.03	8	4.21	0.07	0.968n.s.
LL	14	3.46	0.05	8	3.41	0.03	0.544n.s.
M ¹ B	14	3.67	0.09	8	3.41	0.08	1.905n.s.
LB	14	4.44	0.07	8	4.35	0.08	0.718n.s.
LL	14	2.24	0.03	7	2.27	0.05	0.340n.s.

Significance levels :

t-Test : ** 1% ; * 5% ; n.s. not significant.

TABLE 6

Comparison of *Isaodon m. macrourus* male and female lower tooth measurements (in mm)

Measurement	Males			Females			t
	N	\bar{X}	VAR.	N	\bar{X}	VAR.	
I ₁ M ₁	13	38.87	3.09	5	38.04	0.98	0.985n.s.
I ₁ I ₂	12	4.74	0.04	5	4.62	0.15	0.856n.s.
C ₁ M ₁	13	33.09	2.37	5	31.52	0.43	2.173*
M ₁ M ₁	13	16.50	0.28	6	16.63	0.10	0.552n.s.
C ₁ L	13	3.46	0.93	8	1.91	0.01	4.486**
B	13	1.76	0.10	8	1.12	0.01	5.422**
H	13	4.10	0.34	8	2.51	0.10	7.054**
P ₁ L	15	2.73	0.03	8	2.70	0.01	0.448n.s.
B	15	1.04	0.005	8	1.02	0.002	0.722n.s.
P ₂ L	15	2.94	0.01	8	2.90	0.02	0.791n.s.
B	15	1.35	0.008	8	1.36	0.01	0.245n.s.
P ₃ L	13	3.15	0.04	8	3.20	0.05	0.532n.s.
B	13	1.85	0.03	8	1.81	0.02	0.548n.s.
M ₁ BM	15	2.33	0.02	9	2.32	0.01	0.185n.s.
BD	15	2.76	0.02	9	2.74	0.04	0.287n.s.
L	15	3.56	0.03	9	3.46	0.02	1.460n.s.
M ₂ BM	14	2.92	0.03	9	2.83	0.02	1.301n.s.
BD	14	3.49	0.16	9	3.21	0.08	1.820n.s.
L	14	3.99	0.04	9	3.95	0.02	0.520n.s.
M ₃ BM	15	3.18	0.07	9	3.00	0.01	1.944n.s.
BD	15	3.44	0.20	9	3.03	0.07	2.488*
L	15	4.16	0.06	9	4.28	0.05	1.198n.s.
M ₁ BM	13	3.05	0.08	8	2.85	0.05	1.695n.s.
BD	13	2.57	0.05	8	2.22	0.03	3.772**
L	13	5.03	0.07	8	5.07	0.05	0.355n.s.

Significance levels :

t-Test : ** 1% ; * 5% ; n.s. not significant.

be utilised in taxonomy, especially at the sub-specific levels, no final conclusion can be drawn as to the validity of the two subspecies.

Interrelationships within and between *Isoodon* and *Perameles*

In order to investigate further the interrelationships within the genus *Isoodon*, and also to provide an over-all comparison of these taxa with others of the genus *Perameles*, both grouped and ungrouped specimens of the two genera (see Table 8) were included in multiple discriminant analyses. The first analysis made

TABLE 7

Means and Variances (in mm) for (combined male and female) *Isoodon obesulus* measurements Used in Discriminant Analysis

Measurement	\bar{X}	V.A.R.	Measurement	\bar{X}	V.A.R.
Cranium—(N 10)			Upper teeth (N 14)		
(a) length			P ¹ L	2.31	0.02
Max.	62.52	40.96	B	1.04	0.02
Bas.	57.90	33.40	P ² L	2.37	0.03
Coud.-Bas.	60.78	37.08	B	1.27	0.01
Pal.	37.40	15.21	M ¹ B	2.83	0.04
Nas.	25.63	12.25	L.B	3.22	0.16
Fr.	21.13	2.95	L.L	2.54	0.07
Par.	14.23	2.68	M ² B	3.27	0.04
(b) breadth			L.B	3.37	0.12
Ant. to C	6.72	0.20	L.L	2.75	0.10
at M ²	17.39	1.23	Lower teeth (N 14)		
Ind.-Orb.	18.96	1.98	P ₁ L	2.43	0.05
Mlu. Fr.	12.01	0.16	B	0.91	0.01
Bizyg.	27.81	3.12	P ₂ L	2.67	0.05
Cran.	23.10	2.85	B	1.10	0.01
(c) height			M ₁ BM	1.81	0.03
Ant. to U	5.54	0.30	BD	2.21	0.03
Post to M ¹	15.64	1.29	L	3.10	0.06
Cran.	22.28	4.28	M ₂ BM	2.23	0.03
Occip.	16.06	2.22	BD	2.57	0.01
(d) bulla			L	3.36	0.07
L	10.35	0.43	M ₃ BM	2.38	0.04
B	8.29	0.18	BD	2.55	0.02
(e) varities			L	3.57	0.15
A.P. var. L	4.96	0.06	Mandible (N 10)		
P.P. var. L	7.17	1.21	Max. L	48.14	22.37
P.P. var. B	7.41	0.65	Ramus L	8.51	0.72
			Br at M ₂	3.27	0.13
			Ht. at M ₂	5.01	0.28

TABLE 8

Numbers of Specimens used in Discriminant Analyses

Group	Adults (Skull Analysis)	Adults and Juveniles (Tooth Analysis)
<i>Isoodon m. torosus</i> males	18	24
<i>Isoodon m. torosus</i> females	7*	14
<i>Isoodon m. macrourus</i> males	13	15
<i>Isoodon m. macrourus</i> females	4*	9
<i>Isoodon obesulus</i> (males and females)	10	14
<i>Perameles nasuta</i> males	36	49
<i>Perameles nasuta</i> females	32	53
<i>Perameles gunnii</i> males	19	23
<i>Perameles gunnii</i> females	18	25
<i>Perameles b. notina</i> (males and females)	12	16
<i>Perameles b. bougainville</i> (males and females)	5*	9
Total	174	251

* Run as unclassified individuals to be scored after computation of the discriminant weights.

was based on 26 variates measured for the cranium and mandible; the second trial utilized 23 dimensions of the premolar and molar teeth.

Multivariate analysis of this type allows several groups or populations to be dealt with simultaneously. The technique also permits considerable reduction in the dimensionality of the space in which these groups are treated, from a figure equal to the number of original measurements to a maximum of one less than the number of groups employed (here 8 minus 1 for the skull analysis and 11 minus 1 for the tooth trial). Further, in this reduction to a "discriminant space," there is often little loss of total "information"; i.e. the configuration of groups as plotted on several discriminant functions or axes in the reduced space is not likely to be very different from that obtaining in the original space of greater dimensionality. Often only the first two or three functions computed are necessary to construct a space in which the essential nature of group interrelationships is retained.

(a) *Skull analysis*:—The analysis of 26 measurements of the cranium and mandible taken on eight taxonomic groups of *Isoodon* and *Perameles* would be expected to yield a maximum of seven discriminant functions. However, the first five axes computed are sufficient to account for over 99% of total discrimination and, of this battery, the first two discriminants are most important, contributing 70.8% and 22.6% of total separation, respectively.

Using the first two functions, group centroids for the 8 taxa studied (and 95% probability ellipses to illustrate dispersion for *P. nasuta* males and females) are plotted in Figure 4. It is apparent that considerable separation of the groups in the discriminant space has been achieved. Chi-square output (relating each of the 158 grouped specimens to each of the centroids) was computed according to the procedure outlined in Cooley and Lohnes (1962, pp. 135-136). The results indicate that in fact over 83% (133/158) of cases have been assigned correctly, i.e. lie closer in terms of chi-square "distance" to their own group centroid than to any other. And of the 25/158 misassignments noted, 21 are by sex within species, and four are to the incorrect subspecies (e.g. to *I. m. torosus* rather than to *I. m. macrourus*, or vice versa); no specimens are misassigned at the species or genus level.

These chi-square values can also be used to assess classification of individuals in absolute terms, meaning the extent to which specimens fall within their own expected population distributions and are at the same time excluded from other distributions at some chosen level of probability. Here again, all skulls are excluded at 95% probability from membership in the incorrect species (or genus), though many are not excluded as belonging to the incorrect sex, or subspecies in the case of *I. macrourus*. Only three individuals, correctly excluded from all inappropriate groups, also all beyond the 5% limits of their own distributions as well: these last may be said to be misclassified.

When the several ungrouped specimens (whose measurements were not used in computing the functions) are considered, *I. m. torosus* and

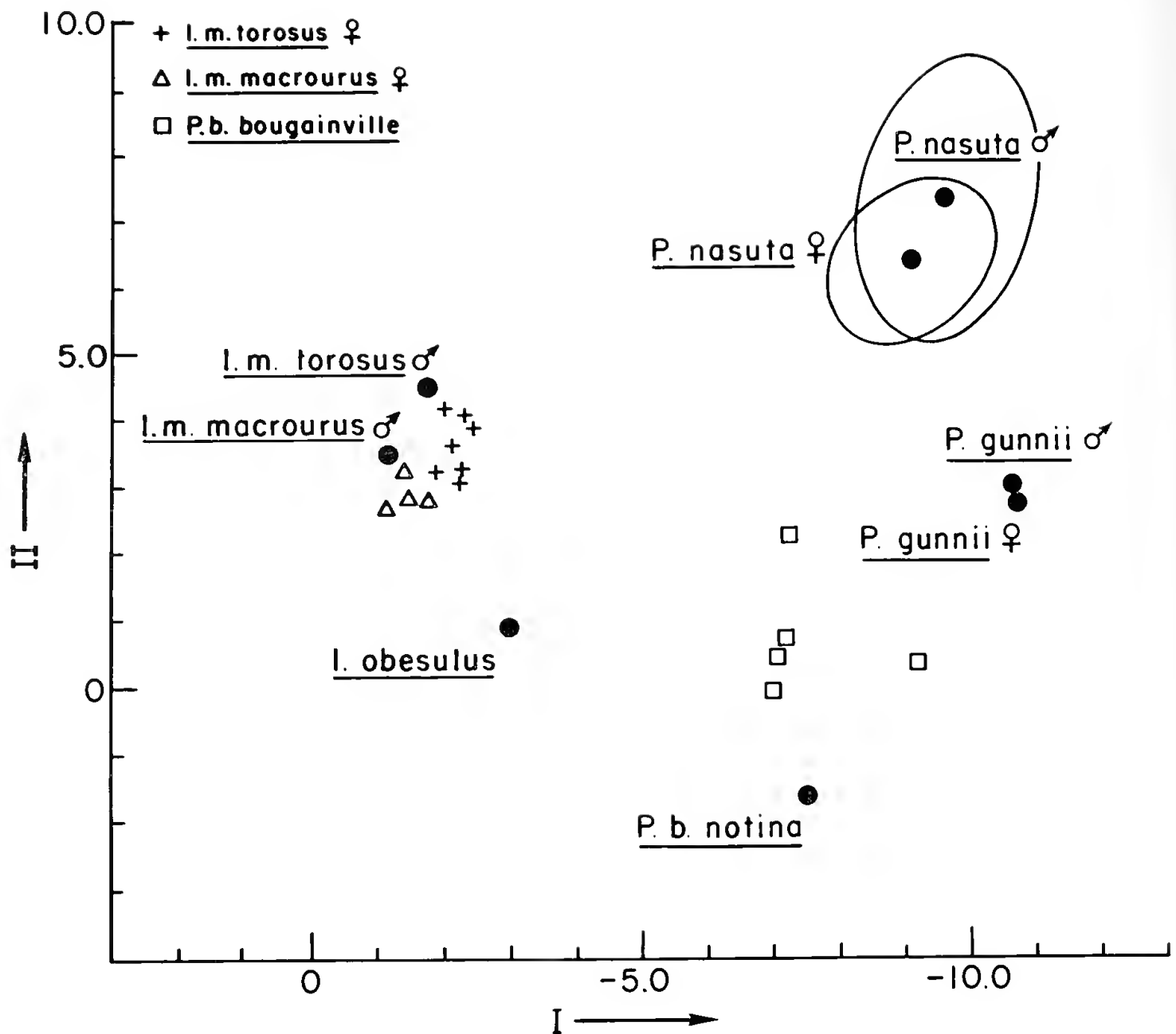


Figure 4.—*Isoodon* and *Perameles* group centroids and individual scores on functions I and II computed from 26 skull measurements; 95% contours illustrating expected dispersions for *P. nasuta* males and females are included.

I. m. macrourus females are seen to lie close to the respective male centroids in the figure, and chi-square data show that, as expected, all are excluded at 95% probability from any save *I. macrourus* distributions. *Perameles bougainville bougainville* individuals, numbering five, are uniformly excluded at 95% probability from all groups, *P. b. notina* included.

Further examination of the centroids plotted in Figure 4 suggests that function I is operating primarily to distinguish *Isoodon* populations from those of *Perameles*, i.e. that this most important contributor to over-all group separation is picking up differences which are of a generic nature. *I. m. macrourus*, *I. m. torosus* and *I. obesulus* tend toward considerably higher (less negative) mean scores (-1.18, -1.77 and -2.99 respectively) on this axis than do the several *Perameles* species, which range between -7.55 (*P. b. notina*) and -10.74 (*P. gunnii* females) on the same scale. Intrageneric dis-

tinctions, either by species (or subspecies) or by sex where males and females have been grouped separately, are not especially apparent.

The relative importance of individual variates to the discrimination afforded by this function may be assessed by reference to the associated scaled vector (Table 9). The elements of the vector correspond to the discriminant weights, but are re-scaled to allow for differences in measurement size and are thus directly comparable (whereas the weights alone are not). Basal length of the skull and inter-orbital breadth seem quite prominent here, the latter receiving the greatest scaled weight of all 26 variables included in the analysis. The negative sign of this weight is as expected, since *Isoodon* species have generally smaller inter-orbital breadths and so should tend toward less negative scores than the *Perameles* groups, as in fact observed. Another significant discriminator is mandibular ramus length, which is weighted

TABLE 9

First and Second Discriminants Computed in an 8-group
Analysis Using 26 Measurements of the Skull

Measurements	Weights		Scaled Weights		F- Ratios*
	Function I	Function II	Function I	Function II	
Max. length	-0.038	0.068	2.206	-3.953	78.99
Bas. length	-0.083	0.141	-4.081	6.872	90.70
Cond. — Bas. length	-0.022	0.046	-1.133	2.318	90.19
Pal. length	0.084	0.309	2.583	9.478	125.46
Nas. length	-0.036	0.017	-0.999	0.466	93.83
Fr. length	-0.009	0.030	0.205	0.659	30.16
Par. length	0.015	0.039	0.284	0.724	90.45
Breadth ant. to C	0.044	0.091	0.322	0.663	68.57
Breadth at M ²	0.035	0.120	0.559	1.910	74.82
Int. — Orb.	-0.417	0.317	-6.171	-4.682	77.57
Min. Fr. breadth	-0.157	-0.041	-1.079	-0.280	102.40
Bizyg. breadth	0.083	-0.052	1.817	-1.155	75.95
Cran. breadth	-0.006	-0.152	0.139	-3.285	29.46
Height ant. to C	0.047	0.135	0.273	0.785	69.14
Height post. to M ¹	0.165	0.417	1.528	3.859	118.02
Cran. height	0.103	0.221	1.622	3.479	61.64
Occip. height	-0.087	0.035	-1.261	0.500	63.00
Bulla length	0.211	-0.458	1.722	-3.737	382.52
Bulla breadth	0.337	-0.115	1.515	-0.517	224.87
A.P. vac. length	-0.131	-0.205	-1.101	-1.723	115.27
P.P. vac. length	-0.119	-0.148	-1.271	-1.580	37.22
P.P. vac. breadth	0.000	-0.190	0.002	-2.049	23.38
Mandible length	-0.009	0.061	0.377	2.553	90.96
Ramus length	0.470	0.147	4.983	1.553	245.46
Breadth at M ₂	0.006	0.175	0.025	0.736	103.55
Height at M ₂	0.139	-0.084	1.152	-0.693	51.52

* Degrees of freedom are 7 and 150.

positively in keeping with the markedly greater values which this variate assumes in the several *Isoodon* (particularly *I. macrourus*) populations measured. Several other measurements, including maximum skull length, palatal length, bizygomatic breadth, cranial height taken posterior to M¹ and from basion to bregma, and length and breadth dimensions of the alisphenoid bulla, also seem important but contribute somewhat less than the aforementioned.

Function II, accounting for only 22.6% of total variance, is evidently operating rather differently. Generic distinctions are here lost completely, as the *Isoodon* taxa have mean scores which lie well within (actually toward the centre of) the range of scores received by the three *Perameles* species represented. However, the *I. obesulus* and *I. macrourus* groups are clearly separated, and the *P. nasuta*, *P. gunnii* and *P. bougainville* populations are also mutually distinct from one another, so that differences within each genus seem to be considerably more apparent on this axis than on function I. Separation by sex is again minor, but the distribution of groups does suggest that "size" is here a factor in discrimination, since the smaller more delicately constructed species (*I. obesulus* and *P. bougainville*) tend to receive low scores and the observed size/robusticity sequence within *Perameles* (*P. nasuta* > *P. gunnii* > *P. bougainville*) is in fact reflected on this discriminant scale.

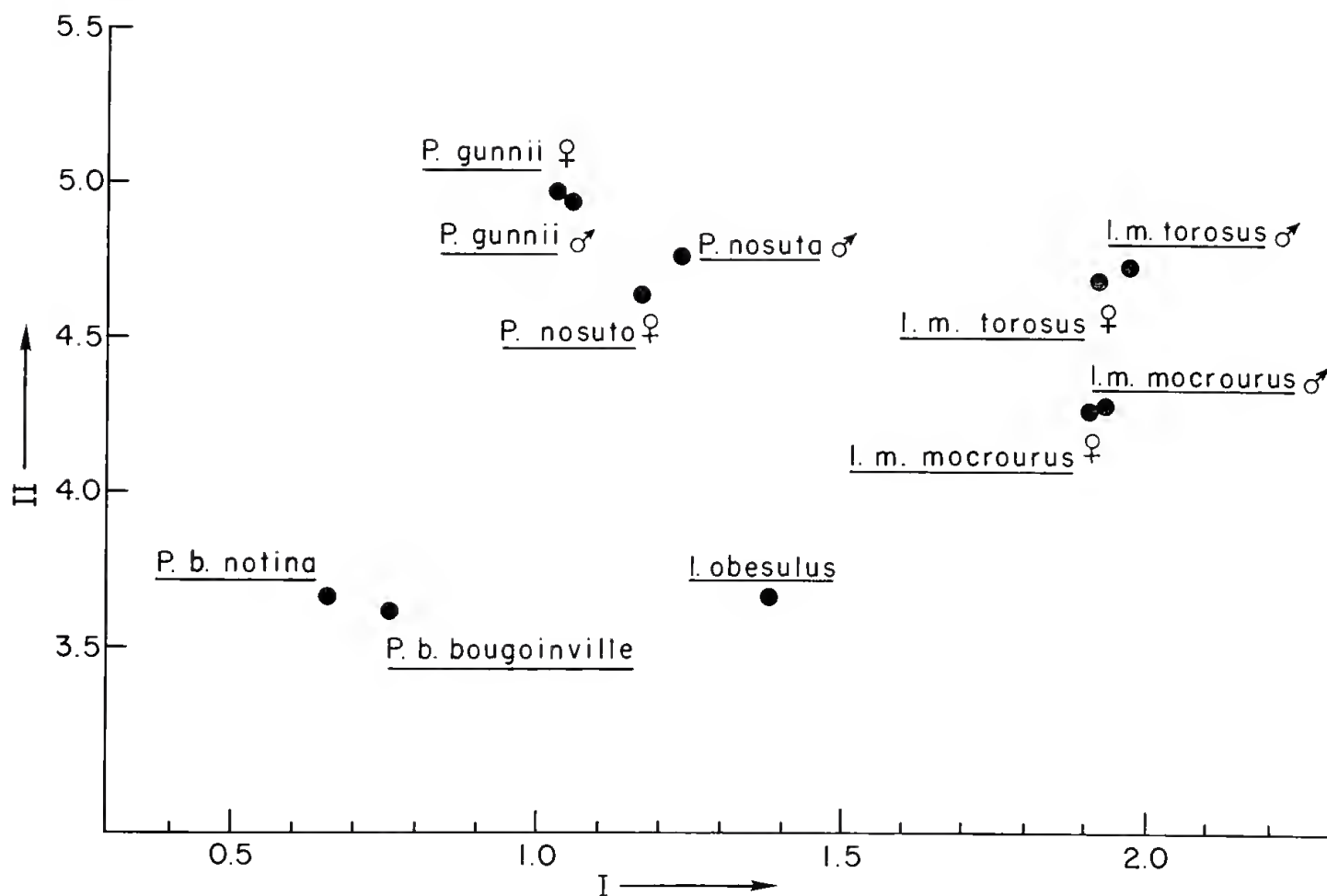


Figure 5.—*Isoodon* and *Perameles* group centroids on functions I and II computed from 23 tooth measurements.

Judging from the scaled weights (Table 9), palatal length and basal skull length are the two variates contributing most heavily to discrimination along axis II, and both are weighted positively. These dimensions are greatest for *P. nasuta* (males and females), smallest in *P. bougainville* and *I. obesulus*, and seem to be good size indicators, so that this weighting is not unexpected. Certain measurements previously seen to be important on function I (e.g. maximum skull length, inter-orbital breadth, cranial height, and bulla length) are also significant here, but others such as ramus length and bizygomatic breadth are de-emphasised, and this second scaled vector is certainly not coincident with the first; this again suggests that the roles played by the several variables are not the same and that discrimination along these axes is effected in rather different ways.

(b) *Dental analysis*:—Owing to the increased sample sizes resulting from the inclusion of certain juvenile specimens, 11 groups of bandicoots could be treated in a discriminant analysis based on premolar and molar tooth measurements. Computation yields a total of ten discriminant functions, each a linear compound of the 23 original variates, but the first seven of these provide more than 99% of overall group separation; functions I and II alone account for some 87% of discrimination, and group centroids on these axes are illustrated in Figure 5.

Inspection of this figure reveals a configuration of groups which is generally similar to that obtained using measurements of the skull, and the level of discrimination achieved is also about the same. Assignments as read from the 11 chi-square values computed for each of the 251 specimens run are correct in 82% (206/251) of cases, and the 45 misassignments recorded are by sex only. Thus in one sense discrimination is actually better here than in the skull analysis, since in fact no individuals are assigned to the inappropriate taxon, even at the level of the subspecies. In absolute terms, all but seven skulls (*P. nasuta* or *P. gunnii*) are correctly excluded at 95% probability from the inappropriate species, though many lie within the territory of a neighbouring (incorrect) sex or subspecies. Eleven specimens are actually misclassified, i.e. lie beyond the 5% limits of their own groups.

The distribution of group mean scores on axis I indicates that, despite the proximity of *P. nasuta* males to *Isodon obesulus*, this first and most important function is acting to separate taxa of *Perameles* from those of *Isodon* and is thus again discriminating genera. However, this (generic) separation is not as clear as in the skull-based analysis, and it seems likely that *I. obesulus* at least is rather less easily distinguished from species of *Perameles* on dental criteria than by reference to the cranium and mandible.

The listing of scaled weights for this function (Table 10) shows that length measurements of certain molars (M^1 , M^2 and M_2) and of P_2 are the more significant contributors to discrimination, whereas dimensions of the other premolars and molar breadths (with the exception of mesial breadth of M_3) have relatively

TABLE 10
First and Second Discriminants Computed in an 11-group Analysis Using 23 Tooth Measurements

Measurements	Weights		Scaled Weights		F-Ratios*
	Function I	Function II	Function I	Function II	
P_1 L	0.091	0.276	0.210	0.635	35.78
P_1 B	0.071	0.126	0.109	0.195	44.35
P_2 L	0.045	0.117	0.095	0.250	50.31
P_2 B	0.060	0.019	0.107	0.034	52.16
M^1 B	0.208	0.145	0.446	0.311	191.91
M^1 LB	0.217	0.385	0.867	1.535	63.02
M^1 LL	0.016	0.054	0.051	0.171	49.79
M^2 B	0.113	0.070	0.359	0.224	138.80
M^2 LB	0.097	0.220	0.337	0.764	61.70
M^2 LL	0.252	0.252	0.762	0.762	96.12
P_3 L	0.121	0.207	0.299	0.512	20.23
P_3 B	0.181	0.034	0.179	0.033	53.91
P_4 L	0.330	0.170	0.737	0.378	37.23
P_4 B	0.069	0.228	0.096	0.313	47.10
M_1 BM	0.110	0.344	0.277	0.865	65.76
M_1 BD	0.060	0.176	0.421	1.238	11.28
M_1 L	0.114	0.009	0.402	0.030	38.34
M_2 BM	0.053	0.068	0.286	0.367	23.18
M_2 BD	0.026	0.043	0.089	0.149	86.34
M_2 L	0.220	0.162	0.689	0.509	79.88
M_3 BM	0.269	0.152	0.591	0.336	207.10
M_3 BD	0.001	0.051	0.002	0.202	69.73
M_3 L	0.133	0.250	0.141	0.829	94.94

* Degrees of freedom are 10 and 240.

minor roles. Of the former, M^2 lingual length, and M_3 mesial breadth, both weighted positively, are consistently greater in average value in populations of *Isodon*, so that these groups tend to have the higher scores. Other variables, which are not such good discriminators at the generic level when considered alone, are evidently acting in combination to effect group separation, but interpretation of these aspects of measurement co-variation is difficult.

If function II is considered alone, the *Isodon*/*Perameles* dichotomy disappears altogether (as in the analysis of the skull), though certain intrageneric distinctions appear to be sharpened. *I. m. torosus* males and females are here removed somewhat from *I. m. macrourus* and *I. obesulus* is again shown to be clearly different from each; the *P. bougainville* groups lie well apart from the other *Perameles* species, though *P. b. notina* and *P. b. bougainville* continue to cluster together. The principal contributors to discrimination on this axis are buccal length of M^1 and distal breadth of M_1 , both weighted positively; and of all the taxa measured, *I. obesulus* and *P. bougainville* are the smallest in these dimensions, which must in large part account for their lower discriminant scores.

The remaining functions (not plotted), which make successively smaller additions to discrimination in other dimensions, appear to alter but little the general configuration of taxa as indicated in Figure 5 and need not be dealt with here.

Conclusions and Summary

The present study of certain taxa of the genus *Isodon* has quantified and highlighted a number of significant features of the skull and teeth

of the group and some of its subdivisions. Notably, *Isoodon* is shown to be characterised relative to *Perameles*, by its broader muzzle, greatly inflated alisphenoid bullae (*P. b. notina* is, however, similar), antero-posteriorly long mandibular rami, small I¹ teeth, broad last premolars and rather squared, compact molars. As in the genus *Perameles*, sexual dimorphism is more apparent in the larger than in the smaller forms. In addition to its value for making taxonomic decisions, with regard to extant populations, the tables of skull and tooth measurements (Tables 1—7), used in conjunction with those previously published (Freedman, 1967 and Freedman and Joffe 1967a and b), should be most useful for identifying and evaluating subsossil and fossil material of the Peramelidae.

The intraspecific analysis of *Isoodon* and the comparisons with *Perameles*, for both of which discriminant analysis was used, have again illustrated the value of this technique for taxonomic studies. On the accepted criteria, the subspecific status of *I. m. macrourus* and *I. m. torosus* could not be unequivocally established solely on the basis of the particular cranial and dental features studied, but the degree of separation achieved in the trial would seem at least to provide important grounds for the full investigation of other characters.

In the 8 group multiple discriminant analysis, based on 26 cranial and mandibular measurements, and in the 11 group analysis, using 23 dental dimensions, the configuration of the *Isoodon* and *Perameles* group centroids is generally similar. However, the skull analysis should provide the more reliable picture of group relationships, as the multiple measurements utilised permit individual skulls to be considered as more meaningful biological entities which can then be dealt with in population terms. In the dental analysis, molar and premolar teeth only are included and it is perhaps surprising, but significant, that the results of this analysis and the one utilizing widespread skull features agree as closely as they do. In both of the above analyses, the first and most important discriminant axis computed serves to separate the *Perameles* taxa from those of *Isoodon*; the additional functions seem to sharpen intrageneric distinctions. This appears to indicate that the generic distinction is here the major one, and that specific or subspecific differences are secondary. Nevertheless, in both analyses *I. obesulus* lies well separated from *I. macrourus* and *P. nasuta* is clearly discriminated from *P. gunnii*. Differentiation of the sexes, where these are treated separately, is always minor and does not appear to be a factor in discrimination.

In both the skull and dental analyses, *P. b. bougainville* and *P. b. notina* lie close together, although in the skull trial the 5 ungrouped *P. b.*

bougainville specimens are excluded from *P. b. notina* at 95% probability. With regard to their relationships to *P. gunnii* and *P. nasuta*, in the skull analysis the *P. b. bougainville* specimens lie rather close to the *P. gunnii* centroids (Fig. 4.), whereas in the dental analysis the centroids of both *P. bougainville* subspecies are well separated from those of the other two *Perameles* species (Fig. 5). Relying principally on the dental analysis, for which sample sizes are considerably larger and in which *P. b. bougainville* has actually been used in computing the discriminant functions, it seems that the closeness of the centroids for *P. b. bougainville* and *P. b. notina* suggests that the two populations most probably only merit subspecific separation, whilst their clear separation in this test from the other two *Perameles* species appears to validate their specific status as a group.

Acknowledgements

The Research Committee, Graduate School, University of Wisconsin, Madison, supported one of us (G.P.R.) as a project associate for the duration of this investigation and also provided funds for the use of facilities at the University of Wisconsin Computing Centre, Madison (Project 3375).

We should like to thank Mr. Don Chandler, Department of Zoology, University of Wisconsin, Madison for taking the photographs for this paper, and Mrs. A. F. Miller, Department of Anatomy, University of Western Australia, Netherlands, for typing the manuscript. Dr. W.D.L. Ride, Western Australian Museum, Perth, kindly read the whole of the manuscript and made several useful suggestions.

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**Journal
of the
Royal Society of Western Australia**

Volume 54

1971

Part 1

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